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Regulation of the shallow limit of giant kelp, Macrocystis pyrifera, at three sites along the Monterey Peninsula

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REGULATION OF THE SHALLOW LIMIT OF GIANT KELP, *MACROCYSTIS PYRIFERA*, AT THREE SITES ALONG THE MONTEREY PENINSULA

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ABSTRACT

REGULATION OF THE SHALLOW LIMIT OF GIANT KELP, *MACROCYSTIS PYRIFERA*, AT THREE SITES ALONG THE MONTEREY PENINSULA

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Abiotic and biotic factors regulating the shallow limit of giant kelp, *Macrocystis pyrifera*, were examined in Monterey Bay, California. Analysis of aerial photographs from 1986 to 1989 indicated that during periods of high water motion the depth of the shallow limit of continuous giant kelp surface canopies was significantly correlated with increases in wave exposure. The depth of the shallowest giant kelp plants between 1993 and 1995 was also correlated with increases in wave exposure. The vulnerability of adult giant kelp plants to removal by water motion appeared to be related to their size. This removal of plants from shallow water also appeared to regulate indirectly the shallow limit during periods of low water motion. Algal turf assemblages were extremely dense in the absence of shading by giant kelp plants, and clearing experiments indicated that the turf inhibited giant kelp recruitment to shallow water. Algal community structure in these shallow subtidal regions appears to be regulated by disturbance-mediated competition; lack of disturbance favoring giant kelp, disturbance favoring algal turfs. Shading manipulations and transplant experiments indicated that the absolute shallowest limit of giant kelp was determined by mortality of giant kelp microscopic stages from high irradiance.

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INTRODUCTION

Factors affecting the distributional limits of species have long intrigued marine ecologists. Connell (1961a, 1961b, 1970, 1972), in his series of classic papers on intertidal zonation, set the stage for numerous investigations of abiotic and biotic factors affecting distribution in marine environments. His hypothesis that abiotic factors (e.g. desiccation or temperature) regulate the upper limit of intertidal species, while biotic factors (e.g. competition or predation) control the lower limits, has become a paradigm in ecology. Though examples exist that contradict Connell's hypothesis in certain situations, his experimental approach remains a stepping stone for research into patterns of species distributional limits.

The economic and ecological importance of kelps (brown algae of the order Laminariales) has been well documented (see Dayton, 1985 and Foster and Schiel, 1985 for reviews). Due to their large size, rapid growth and recruitment capabilities, and potential for long-distance dispersal, kelps are often dominant competitors for light and space in temperate and polar regions around the world (see Lüning, 1990 for review). Surface canopy kelps of the genus *Macrocystis* have been of particular interest, probably because of the importance of these kelps and the flora and fauna associated with them to local economies. Given the great interest in *Macrocystis*, however, surprisingly little is known about the factors regulating its distributional limits.

The giant kelp, *Macrocystis pyrifera* (hereafter, giant kelp), ranges in the Northern Hemisphere from Año Nuevo Island, in central California, to Punta Asuncion-Punta San Hipolito in Baja California, Mexico (Foster and Schiel, 1985). Its surface canopies have been described from as shallow as 4 m to deeper than 30 m, and populations are usually characterized as subtidal (Foster and Schiel, 1985). A few studies, however, have shown that giant kelp in the Southern Hemisphere may

predominate in the lower intertidal zone (Barrales and Lobban, 1975 - Argentina; van Tussenbroek, 1989 - Falkland Islands; Westermeier and Moller, 1990 - Chile) and isolated low intertidal plants have been observed in California (North, 1971; M. S. Foster, pers. comm.; pers. obs.). Thus, information about factors affecting the upper (shallow) subtidal limits of giant kelp may help explain geographic variation in giant kelp distributions.

The shallow limits of giant kelp in central California are seasonally variable (see **Results: Shallow limit vs. abiotic factors**). Although many factors may account for this variation (e.g. grazing, growth differences, temperature, and recruitment), the increased loss of canopy during winter suggests a probable relationship between shallow limits, giant kelp mortality, and seasonal fluctuations in water motion.

The hypothesis that exposure to swell regulates the shallow limit of giant kelp is not new. Numerous studies have stressed the importance of water motion to the mortality of giant kelp in California (North, 1971; ZoBell, 1971; Rosenthal et al., 1974; Gerard, 1976; Foster, 1982; Dayton et al., 1984; Reed and Foster, 1984; Tegner and Dayton, 1987; Harrold et al., 1988). All of these studies, however, based their inferences on qualitative estimates of wave exposure. Seymour et al. (1989) were the first to determine wave exposure quantitatively (based on monitored significant wave height and period data) in kelp mortality analyses and suggested that breaking waves may set the shallow limit of giant kelp. Foster and Schiel (1985) also proposed that increased frequency and magnitude of storm events in the northern latitudes may be partly responsible for determining the northern limits of giant kelp populations in California.

Aerial surveys in central California also commonly show a distinct subtidal zone, shoreward of the giant kelp surface canopies, where giant kelp is never present. North (1971) indicated that increased water motion may account for the absence of giant kelp

in this region. Seymour et al. (1989) showed that the mortality of giant kelp plants increased significantly with decreasing depth and attributed this to the effects of increased drag due to entanglement. Since entanglement probably increases with an increase in drifting plants during storms, swell events are probably an integral part of both hypotheses. However, the separate effects of water motion and entanglement with drifting plants have yet to be examined.

Shallow limits may also be affected by processes that influence other giant kelp life history stages. Recruitment may be affected by sand scour, pollution, substrate availability, temperature, nutrient concentrations, grazing, and competition. Santelices and Ojeda (1984) demonstrated through the experimental removal of *Lessonia vadosa*, present in a dense belt shoreward of the upper limit of giant kelp in Chile, that giant kelp was able to extend it's upper limit into shallower water when *L. vadosa* was removed. Reed and Foster (1984) found increased recruitment of giant kelp within clearings of geniculate coralline algae, and suggested that the branches of these corallines either directly impeded the settlement of kelp spores or reduced irradiance below levels normally needed to initiate gametogenesis and sustain growth. Although this study did not specifically address the shallow limits, it demonstrated the ability of geniculate coralline algae to inhibit kelp recruitment.

Harrold et al. (1988) found that along with the exposure gradient they investigated in Monterey, there was also a gradient in the density of geniculate coralline and foliose red algae. Exposed sites had dense algal turf assemblages consisting almost entirely of two species of geniculate coralline algae, *Calliarthron cheilosporioides* and *C. tuberculosum*. *Calliarthron* spp. were present in the algal turf assemblage at the protected sites, but densities were relatively low. Foliose red algae decreased in density as wave exposure increased. These dense algal turfs may inhibit the recruitment of giant kelp to shallow water along the Monterey Peninsula.

Wave exposure and inter-specific competition may both affect the shallow limit of giant kelp. However, the stochastic nature of these factors coupled with the consistent exclusion of giant kelp from waters less than 2 m depth along central California (unpublished aerial photographic data), suggests that more constant factors, such as high irradiance, may be inhibiting giant kelp above 2 m. Although ultra-violet radiation is attenuated below 2 m depth, it does account for a significant amount of spectral energy in shallow water (Smith and Baker, 1979). Irradiance of visible light is also extremely high in shallow water (see **Results: High irradiance**). Giant kelp zoospores lack cell walls (Henry and Cole, 1982) and may be extremely vulnerable to these high radiation levels. Consequently, high mortality of giant kelp microscopic stages from high irradiance may determine the absolute shallow limit of giant kelp.

Pilot studies indicated giant kelp gametophytes suffer 100% mortality when exposed to ambient sunlight for short durations (unpublished data). Although no studies have documented this phenomenon for giant kelp in the field, the hypothesis is supported by Anderson (1965) who observed bleaching of bladelets (< 2 cm) on the upper portions of vertical transplant ropes seeded with giant kelp spores. Wood (1987) also reported high mortality of *Ecklonia radiata* sporophytes following the removal of *Ecklonia radiata* canopies, and attributed this to high levels of UV radiation.

Data, therefore, suggest that wave exposure, competition, and high irradiance may be especially important to the shallow limits of giant kelp. To investigate further the effects of these processes, I addressed the following questions with field surveys, and laboratory and field experiments: Does wave exposure cause temporal and spatial variability in the shallow limit of giant kelp along the Monterey Peninsula? Does inter-specific competition with turf algae inhibit recruitment of giant kelp to shallow water? Does photodamage from high irradiance inhibit giant kelp recruitment at depths less than 2 m?

METHODS AND MATERIALS

Study sites

Three sites were chosen to investigate the effect of wave exposure and inter-specific competition on the depth of the shallow limit of giant kelp within Monterey Bay, California. A wave exposure gradient was proposed based on previous work (Harrold et al., 1988; Graham et al., in preparation), extending along the north coast of the Monterey Peninsula from Otter Point (OP; most exposed) to Lovers Point (LP; intermediate) to Monterey Bay Aquarium (MBA; most protected; Figure 1). Daily significant wave height measurements consistently show that Point Joe experiences the full force of westerly, northwesterly and southwesterly swells. As swells travel into the bay, most of those from the southwest are blocked by Point Pinos while those from the west and northwest undergo various levels of refraction. Consequently, OP (roughly halfway between Point Joe and MBA) and LP (roughly halfway between OP and MBA) tend to experience smaller significant wave heights from incident swells than Point Joe, with the lowest level of wave exposure along the gradient at MBA.

Wave exposure levels (i.e. exposed, intermediate, protected) could not be replicated due to the lack of additional wave exposure gradients near the study area. Moreover, because of poor interspersion of wave exposure levels along the gradient, this wave exposure gradient could not be broken up into multiple exposed, intermediate, and protected sites. Consequently, to avoid pseudoreplication, statistical differences among sites were treated as location effects rather than wave exposure effects (Hurlbert, 1984). However, I attempted to isolate wave exposure from confounding factors (e.g. substrate composition, bottom topography, bottom temperature) by choosing sites as similar as possible in all respects except exposure to breaking waves.

Two additional study sites, Monterey Harbor and Stillwater Cove, were used for transplant experiments to test the effect of high irradiance on giant kelp recruitment to shallow water (Figure 1). The Monterey Harbor site was on a cobble shore (~ 2 m depth) just inside the breakwater. This area was close to the opening of the harbor, and water clarity and lack of obvious pollution suggested it was well flushed. This site was chosen because it was protected; experimental apparatus remained securely in place. The sites at Stillwater Cove were two rocky plateaus (~ 10 m depth) from which all giant kelp plants had been removed within a 15 m radius circle. The two sites were approximately 100 m apart and exposed to similar winds and swells.

Abiotic factors

Many characteristics of wave exposure may be estimated from pressure sensed values of significant wave height and wave period. Of these, horizontal orbital displacement (D_H) and breaking depth (BD) may be the best for determining the effects of wave exposure on giant kelp populations. D_H estimates the distance water particles travel in the horizontal direction and can be quantified using linear wave theory (Denny, 1988). As D_H increases, giant kelp canopies may move in the same direction for longer periods of time. If D_H is long enough to stretch a giant kelp plant taut, than a force will be placed on the holdfast and stipes by the drag of the surface canopy biomass. This parameter may be a good predictor of giant kelp moralities resulting from structural failures due to tension.

Depending on bottom topography, BD usually occurs along a gradient perpendicular to the shoreline (i.e. larger waves break in deeper water and farther offshore than smaller waves). This parameter may be an excellent predictor of nearshore kelp mortality since it is the best estimate of the location where turbulence caused by the breaking waves are imposed on the surface canopy. If D_H is long enough

to stretch giant kelp plants taut in the onshore direction, giant kelp plants may be more vulnerable to breaking waves. The combination of D_H and BD are most likely responsible for the majority of kelp moralities in the shallow water (Seymour et al., 1989). Onshore winds may also bias giant kelp canopies in the onshore direction, and thereby contribute to giant kelp mortalities. Consequently, giant kelp distributions may be limited by a combination of all of these abiotic factors and the occurrence of storms (i.e. long D_H, deep BD, and high onshore winds) may prove to be the best predictor of the depth of the shallow limit of giant kelp.

Continuous wave height and period estimates were obtained from an S4 current meter anchored at 10 m depth within 200 m of the MBA site between November 1985 and June 1994. Wave spectra were collected four times daily as 28 consecutive ensembles of 256 pressure measurements sampled at 0.5 s intervals. Significant wave height (H_S; average height of 1/3 largest waves) was calculated as 2.83 x $\sqrt{}$energy variance of the 28 time series (Kinsman, 1965) after correction for high frequency attenuation using a pressure transfer function (W. Broenkow, pers. comm.). The four measurements were averaged to give mean daily H_S. This instrument failed in June 1994, so relationships with offshore buoys (Coastal Data Information Program, 1994-1995) were obtained and used to extrapolate missing data until April 1995.

H_S and period estimates at OP and LP were for shorter durations than at MBA, and were made using portable pressure transducers (Ocean Sensors, Encinitas, CA) anchored at 15 m depth. H_S and period were measured three times daily and each wave data record consisted of 512 pressure measurements sampled at 2 s intervals. H_S was calculated as 4 x standard deviation of the pressure record after correcting for the effect of a non-static water column (Denny, 1988), and the three measurements were averaged to estimate mean daily H_S. H_S and period were estimated at OP for 478 days between April 1988 and October 1991, and at LP for 52 days between May and June 1995.

Due to the limited data at LP, H_S and period estimates at this site were used solely to corroborate its distinction as intermediate wave exposure along the proposed gradient. H_S and period estimates from OP and MBA, however, were used to examine the relationship between the depth of the shallow limit of giant kelp and wave exposure. H_S estimates at LP and OP were shoaled to 10 m depth, using linear wave theory, to allow comparisons with MBA. A significant regression between data from the portable sensor at OP and the permanent sensor at MBA was obtained (OP = -0.03 + 1.76 x MBA, n = 355, $r^2 = 0.92$; see **Results: Gradients**) and used to extrapolate missing data at OP.

A FORTRAN program provided by Dr. E. Thornton (Naval Postgraduate School, Monterey, CA) based on the "bore dissipation model" of Thornton and Guza (1983) was used to model wave exposure (Appendix 1). This program estimated BD and H_S at breaking, from mean daily H_S and period estimates, by shoaling H_S along a known bathymetry which was corrected for changing tides. Thus, it theoretically predicted the location of the breaker zone and height of breakers for any given day. D_H was estimated from H_S at breaking and period (Denny, 1988; Appendix 1). Depth vs. distance profiles were used as bathymetries for OP and MBA, thereby correcting wave exposure estimates for among-site differences in topography. BD and H_S were computed from this model using mean daily H_S and period estimates at OP and MBA between March 1986 and September 1989, and November 1993 and April 1995.

Average daily bottom temperature was measured at OP and MBA between April 1987 and September 1989. The temperature recording device at OP was within the pressure transducer unit and the temperature data record was subject to the same limitations as H_S and period data. The temperature data from MBA, however, were nearly continuous. Average daily wind velocity (m/s; positive values represent onshore

flow, negative values represent offshore flow) was measured at MBA between March 1986 and September 1989, by an anemometer on the roof of the Monterey Bay Aquarium. Minimum daily tidal heights were measured at MBA between March 1986 and April 1995. Minimum daily tidal heights were used for the wave shoaling program because they estimated the shallowest depth of the water column, and therefore the deepest BD values for each day.

Depth of shallow limit

Variation in the shallow limit of giant kelp may be viewed in terms of two variables: distance from shore, and depth. In most nearshore regions, depth increases with increasing distance offshore and the discrimination between the variables may seem trivial. However, wave exposure, light, and temperature, the factors most often attributed to regulation of algal distributions, are all largely affected by changes in depth. Depth estimates are also much easier to obtain than distances offshore. Consequently, depth estimates will probably yield the most precise and direct assessment of the shallow limits of giant kelp, and were therefore used during this study.

The OP-LP-MBA wave exposure gradient was used for a detailed examination of the dynamics of the shallow limit of giant kelp. This part of the study was two-fold. First, the depth of the shallow limit was estimated at each site using aerial canopy photographs taken between March 1986 and September 1989 (hereafter, the photo study). Second, the depth of the shallow limit was estimated at each site *in situ* using SCUBA, between December 1993 and April 1995 (hereafter, the field study).

Aerial canopy photographs, used during the photo study, were obtained for each site (EcoScan, Watsonville, CA). Photographs were taken using infrared film (Ektachrome, Kodak) from an altitude of 2500 m during periods of similar tidal, sea and weather conditions. Only plants with surface canopies could be located using the aerial

photographs. Transparencies were projected onto a wall and adjusted to scale using distances between known landmarks. To randomly locate the shallowest giant kelp plants for the photo study, one permanent 60 m transect was positioned on the canopy maps parallel to shore at each site along the historically shallowest limit of giant kelp surface canopies (i.e. the shallowest limit between March 1986 and September 1989). Ten bearings were run offshore at random distances along each permanent transect. The distance to the first plant with a surface canopy was recorded for each bearing and its depth was predicted from observed distance vs. depth profiles. Among-site differences in distance vs. depth profiles resulted in many instances where single photographs did not represent the entire kelp population at a given site. Therefore, the maximum depth that could be estimated for the shallow limit was standardized to 8 m. Thus, this method occasionally underestimated the true depth of the ten shallowest plants at LP and OP when giant kelp surface canopies were in deep water. Surveys were done monthly from March 1986 through September 1989 at each site.

To randomly locate the shallowest giant kelp plants for the field study, the permanent 60 m transects used during the photo study were positioned at each site based on landmarks identified from the aerial canopy photos. The transects were marked with stainless steel hardware. Bearings were run offshore, perpendicular to the shoreline, at random distances along the permanent transects.

Depth, number of fronds (> 2 m long), relative age (recruits had few fronds, few dichotomies, and did not form a surface canopy) and canopy condition (presence or absence of a surface canopy) was noted for the first giant kelp plant reached that fell within 1 m of either side of the diver's bearing. After the first plant was located the diver then returned to the permanent transect and continued until 20 bearings had been sampled, to locate 10 plants with surface canopies and 10 plants without surface canopies. The distances along the permanent transects were stratified to insure proper

interspersion of the sampling units (i.e. plants). Plants were rarely observed along the shoreward side of the permanent transects (only 14 out of 1000 plants throughout the study), but when observed they were sampled in lieu of plants on the seaward side of the transects. This resulted in estimates of depth and number of fronds for the 20 plants closest to the permanent transect, 10 plants with surface canopies and 10 plants without surface canopies. From these estimates, the depth of the 10 shallowest plants overall was used to estimate the depth of the shallow limit. A pilot study found that a sample size of 10 gave the most cost efficient and precise estimate of depth relative to a maximum sample size of 20. Depths were estimated in feet using calibrated dive computers, converted to meters, and standardized to MLLW using tide tables.

Sampling frequency was determined by the occurrence of favorable dive conditions. I attempted to sample all three sites on the same day, but extreme wave conditions prevented sampling OP during early April 1994 and often forced me to sample this site 1 - 2 weeks after MBA and LP. MBA and LP were sampled 17 times and OP 16 times between December 1993 and April 1995.

Many factors (e.g. photographic resolution, weather conditions, and water clarity) limited my ability to identify individual plants during the photo study. Consequently, most of the plants identified for shallow limit estimates during the photo study were along the shoreward edge of the continuous giant kelp surface canopy (Figure 2). These plants were probably never the same ones that would have been observed during the field study, but because of the different timespans of the two studies and the lack of simultaneous photo and field estimates that cannot be guaranteed. My observation that continuous giant kelp surface canopies were absent within the regions where plants were sampled for the field study (Figure 2), supports this hypothesis. Therefore, I feel that the depth of the shallow limit estimated during the photo study best describes the depth of the shallow limit of the continuous giant kelp surface canopies at

each site (hereafter, canopy shallow limit or canopy SL), whereas those plants observed during the field study represent the depths of the shallowest plants in the entire study site. These are referred to as the surface SL (depth of the 10 shallowest plants with surface canopies), subsurface SL (depth of the 10 shallowest plants without surface canopies), and overall SL (depth of the 10 shallowest plants overall). The distinction between these four shallow limit estimates is important, as they will be compared and contrasted throughout this paper.

Inter-specific competition

Observations indicated that turfing algae dominate the shallow subtidal (1-4 m below MLLW) regions at OP, LP, and MBA. Giant kelp is not common at these sites at depths shallower than 4 m and appears to be limited to areas in which algal turfs have been removed. Experiments were done at each site to test the hypothesis that algal turfs inhibit the recruitment of giant kelp to shallow subtidal regions.

Three 0.5 m^2 clearings and replicate control plots were interspersed in an alternating, systematic fashion along the permanent transects which marked the historically shallowest limit of giant kelp at each site (see transect description above). Plots were placed on the first suitable substrate (granodioritic outcrops larger than 1 m^2) located shoreward of random distances along each transect. Clearings were made in late May 1994 by scraping the substrate with the flat edge of a sledgehammer. This method was used because it removed most sessile invertebrates and all algal blades from the substrate, but left crustose algae (non-geniculate coralline algae and holdfasts of fleshy/geniculate coralline algae) intact, thus mimicking natural disturbance to algal turfs caused by moving boulders (pers. obs.). One corner of each plot was marked with a plastic rivet.

Density of giant kelp recruits and macro-invertebrate grazers were estimated using a 0.25 m^2 PVC quadrat placed within each plot at a random distance and bearing from the rivet. The quadrat contained crisscrossed strings forming 16 systematically placed intersections under which percent cover of algae, bare substrate, and sand was estimated by counting the number of intersections contacted out of 16. This resulted in a spatial resolution of 6.25%. All algal species observed within the 0.25 m^2 quadrat but not recorded as a contact were noted as rare. All plots were sampled every 1-3 months. The random placement of the quadrats within the plots limited the probability that the same exact spot would be sampled on subsequent dates. All macroalgae and macroinvertebrate grazers were identified to species except gastropods, which were identified to genus, according to Abbott and Hollenberg (1984) and Morris et al. (1980). Many algal species were later analyzed at the genus level since congeners were often rare and statistical analyses inappropriate. Bare rock is rare at the three sites and crustose algae cover most of the substrate (Harrold et al., 1988; pers. obs.). Both were recorded as bare substrate, since giant kelp recruitment is not inhibited by crustose algae (Reed and Foster, 1984; pers. obs.).

Natural disturbance to algal turfs was monitored bimonthly at each site from September 1994 to April 1995. The percent cover of all macroscopic algal species, bare substrate, and sand, as well as the density of macroinvertebrate grazers was estimated using the quadrat method described above. Seven quadrats were randomly placed along the permanent transect at each site during each sampling period.

Irradiance

During laboratory pilot studies it was observed that giant kelp gametophytes suffered 100% mortality when exposed to ambient sunlight for short periods. A series

of laboratory and field experiments were done to test the hypothesis that high irradiance inhibits the recruitment of giant kelp to shallow water by killing microscopic stages.

Due to difficulties in inoculating substrate in the field, the effect of high irradiance levels on the settlement and germination of giant kelp spores was tested in the laboratory. Shading manipulations were created from 7.5 x 16.5 cm PVC tubing covered with Mylar® plastic (frame in Figure 3). Two grades of carbon screening were added to create low irradiance (23% transmission) and mid irradiance (53% transmission) treatments. A Mylar only treatment served as a high irradiance treatment (97% transmission), while a fourth treatment had no covering and served as a control for the Mylar (100% transmission). Five replicates of each treatment were randomly placed into a 350 liter outdoor tank exposed to ambient sunlight. Treatments were placed in areas of the tank that were not shaded by the tank walls. A flow rate of 0.33 liters/second of filtered (5 μm) seawater provided ambient temperature, nutrient and salinity levels. Water level was maintained at 0.66 meters depth. Light measurements were made beneath each treatment using a LICOR 190S cosine collector quantum irradiance meter.

To test the effect of high irradiance on spore settlement, one glass slide was placed under each shading treatment. A spore suspension was obtained from giant kelp sporophylls by the methods of Reed (1990; as were all inoculations during the field experiments) and released into the tank at sunrise, resulting in an effective tank concentration of 7×10^5 spores/ml. All slides were collected at night, 36 hours after inoculation. Spore densities were determined by counting all germinated spores visible in 11 randomly placed fields of view (400x), measuring 0.16 mm^2. This method was found to give an absolute precision of $\pm$ 1 spore/0.16 mm^2.

Two transplant experiments were conducted in the field to test the hypothesis that high irradiance limits the survival of giant kelp gametophytes and embryonic

sporophytes in shallow water, and to determine which life-history stage was most vulnerable to high light irradiance. In the first experiment, light was directly manipulated *in situ* using shades. Shade frames were made out of PVC tubing and were 7.5 cm tall and 16.5 cm wide (Figure 3). Three treatments were created; roof control (shade frame only), high light [shade frame plus a 3 mm thick acrylic cover (95% light transmission)], and low light [shade frame plus an acrylic cover coated with adhesive car window tinting (20% light transmission)]. One shade of each treatment was attached to experimental platforms made from large concrete parking lot bumpers and 2.5 x 20 x 102 cm wooden planks (Figure 3) in a randomized block design with platforms serving as blocks. Three platforms were placed at a depth 0.5 m below MLLW in Monterey Harbor, where giant kelp plants were growing in deeper water (~ 2 m below MLLW; see above).

Giant kelp gametophytes and embryonic sporophytes were isolated onto 11.5 x 11.5 cm acrylic plates (roughened with coarse-grade sandpaper). Three experimental trials were run in Spring 1995. Each trial consisted of placing nine plates of the same life-history stage under the shades. The third trial used plates onto which no life-history stage had been cultured. The experiment was monitored weekly to remove the few grazers that wandered onto the platforms and to remove fouling organisms from the shades. Sporophyte density was sampled one week after sporophytes were first observed on the plates. To reduce edge effects, sporophytes were only sampled within a 5 cm x 5 cm region in the center of the transplant plates. The settlement plates were only exposed to air briefly (< 1 minute), and kept cool and in the dark during transport from the laboratory.

In the second experiment, polypropylene rope was seeded with giant kelp spores in the laboratory and transplanted to various depths at two sites within cleared giant kelp canopies in Stillwater Cove (see above). This allowed the natural attenuation of light

with depth to be used to manipulate irradiance. Two different life history stages (gametophyte and embryonic sporophyte) were isolated onto 10 cm long polypropylene ropes. A third rope was kept clean to control for natural recruitment. One rope per treatment (gametophyte, embryonic sporophyte, and control) was placed every meter along the upper 7 m of 10 m vertical lines buoyed taut at MLLW at the two sites within the cove (3 lines per site). Due to limited culturing facilities the embryonic sporophyte treatment could only be deployed at one site. The position of treatments within each 1 m segment was randomized. All buoy lines were placed a minimum distance of 6 m apart. Presence of visible giant kelp sporophytes was determined *in situ*, one week after the first sporophytes were observed in each treatment. This was after four weeks for the sporophyte treatment, six weeks for the gametophyte treatment, and eight weeks for the control treatment.

Relative water motion was estimated using spherical clod cards made from a mixture of 50% Plaster of Paris and 50% latex paint. These were allowed to harden around 5 cm stainless steel eyebolts. The clod cards were dried, weighed, and attached every meter along the upper 7 m of each buoy line at each site. The clod cards were removed after four weeks, redried, and reweighed. Relative water motion was estimated as the decrease in clod card weight (in grams). Irradiance, salinity, and temperature were measured every meter with a handheld CTD (Seacat, Seabird Electronics, Bellvue, WA), equipped with a 4π quantum irradiance meter, at each site several times during the study. The sensor measured photosynthetically active radiation (PAR; 400 - 700 nm).

Statistical analyses

Linear regression, t-tests, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) were used to test the various hypotheses investigated during the study. Factors were fixed in all cases. Alpha levels were set at 0.05. Multiple

comparisons were controlled for experimentwise error inflation rate using the Dunn-Sidák method [$a' = (1 - (1 - a)^{1/r})$, where r is # comparisons being made; Day and Quinn, 1988]. The assumption of homoscedasticity was tested using Cochran's test. When transformations were necessary, they were successful in correcting heteroscedastic data. Percent cover estimates were arcsine transformed and densities were square root transformed. However, due to layering, maximum percent covers often exceeded 100%, in which case square root transformations were used. It was assumed that the statistical tests would be robust to any deviations from normality that were not corrected by the transformations (Underwood, 1981). Residuals were analyzed to test the assumptions of normality and homoscedasticity of error terms for linear regressions and ANCOVA.

RESULTS

Gradients

H_S was significantly greater at OP than at LP, and H_S at LP was significantly greater than at MBA. The relationships between H_S estimated by the portable sensors placed at each site (dependent variables) and the permanent sensor at MBA (independent variable) were linear (Figure 4). The y-intercepts were near zero, suggesting that among-site differences in the relationship between the independent and dependent variables were due primarily to the slopes. The slope of the relationships increased from MBA to OP. The slopes were significantly different (ANCOVA; Site x permanent sensor [Covariate]; $F = 60.66$, $df = 2, 434$, $p < 0.0001$; multiple comparisons, OP > LP > MBA). The 1:1 relationship between the portable sensor placed at MBA and the permanent sensor at MBA indicates that the two sensors were estimating H_S similarly (Figure 4).

Differences in H_S between MBA and OP were determined for days when H_S was measured at both sites simultaneously (Figure 5). H_S was always greater at OP than at MBA (Figure 5b) and the between-site differences were significantly greater than zero (paired t-test; $t = 35.51$, $df = 354$, $p < 0.001$). H_S's greater than 1 m were rare at MBA but common at OP (Figure 5a). H_S from LP were not used in this analysis due to the absence of simultaneous H_S measurements at LP and OP. However, the limited data set suggests that H_S at LP was always greater than at MBA. These results and those from the ANCOVA indicate that for any given day, H_S increases from MBA to LP to OP. Although numerous parameters could have been used to quantify the wave exposure gradient (e.g. D_H, H_S at breaking, BD), H_S is the most common parameter available and is relatively easy to compare among studies.

While sites varied in water temperature, this variation was slight. A significant linear relationship in average daily bottom temperature existed between OP and MBA [linear regression; OP = 0.14 + (0.96 x MBA), df = 443, $r^2 = 0.82$]. Temperatures greater than 15.0 °C at either site occurred only once in 444 days. MBA was an average of 0.3 °C warmer than OP, and warmer 77% of the time, but these differences were rarely greater than 1.0 °C. Also, these weak temperature differences contradict the wave exposure gradient relative to possible negative effects on giant kelp (i.e. MBA is characterized by higher temperatures and is more protected from wave exposure).

Sand cover fluctuated according to spatial and temporal variability in wave exposure (Figure 6). On each sampling date MBA had the greatest cover of sand followed by LP and OP; however this gradient in sand cover was never significant. Sand cover was low at all three sites during the winter months, and greatest in September 1994. Sand cover was generally low and did not account for greater than 16% cover at any site during this study.

Bottom topography was similar at the three sites (Figure 7). Depth increased linearly with increasing distance offshore at each of the sites. The rate of increase was linear, but steeper at LP than at MBA and OP, with a depth of 9 m attained ~ 175 m offshore at LP, and ~ 310 m offshore at MBA and OP. These differences were accounted for by the methods used to estimate the depth of the shallow limit, and wave exposure. High relief rocky outcrops were present, but rare, at each site.

Shallow limit vs. abiotic factors

The depth of the canopy SL varied among sites and dates between March 1986 and September 1989 (significant Site x Date interaction; Table Ia; Figure 8a). The canopy SL was deepest during winter months and shallowest during summer months at each site. The depth of the canopy SL increased from MBA to OP throughout the study.

Temporal variability in the depth of canopy SL differed significantly among the sites [variance among dates (m^2); MBA = 0.17, LP = 0.45, OP = 0.65; Cochran's test for equal variances, C = 0.51, df = 43, $p < 0.05$], indicating that the canopy SL became less stable from MBA to OP.

As expected, the various parameters chosen to estimate wave exposure at MBA and OP (D_H, H_S at breaking, and BD) were highly correlated (Table II; Figure 9a), with between-site differences like those for H_S. These factors were also positively correlated with average daily wind velocity at MBA (Table II; Figure 9b). Storms generally exhibited large D_H, large H_S at breaking, deep BD, and high onshore wind velocities.

Collinearity among abiotic factors made it impossible to separate the relationships between individual abiotic factors and depth of the canopy SL. Consequently, D_H was used as an indicator of storms and tested against the depth of the canopy SL using linear regression because D_H was the best predictor of canopy SL depth. Maximum D_H was determined every 7, 14, 21, and 28 days prior to canopy SL depth estimates, and each was tested against the depth of the canopy SL at MBA and OP using linear regression. Bi-weekly (14 days) maximum D_H was the best predictor of the depth of the canopy SL at both MBA and OP (Table IIIa; Figure 8b). The positive correlation between D_H and depth of the canopy SL was better at OP than MBA. Deeper canopy SL depths occurred during periods of large D_H at both sites, and therefore during periods of high storm activity.

The depth of the surface SL and overall SL varied among sites and dates between December 1993 and April 1995 (significant Site x Date interactions; Table Ib-c; Figure 10a-b). Depths of the surface SL and overall SL were highly correlated at each site, with surface SL depth estimates overestimating the depth of the overall SL (Table IIIb).

Fluctuations in the depth of both the surface SL and overall SL were similar to those observed for the canopy SL (Figures 8a and 10a-b). The surface SL and overall

SL were deepest during winter months and shallowest during summer months at each site (Figure 10a-b). Multiple comparisons made during periods of maximum and minimum depths of the shallow limit indicate significant among-site differences in the surface SL during January 1995 and in the overall SL during February and September 1994 and January 1995 (Figure 10a-b). Temporal variability of surface SL and overall SL depths were also similar to that of canopy SL, significantly increasing from MBA to OP [variance among dates (m^2); canopy SL: MBA = 0.19, LP = 0.21, OP = 0.61; overall SL: MBA = 0.12, LP = 0.14, OP = 0.40; Cochran's test for equal variances in both cases, C = 0.60, df = 16, $p < 0.05$].

Unlike the canopy SL, among-site differences in the depth of both the surface SL and overall SL were opposite between winter and summer months. Depth of the surface SL and overall SL increased from MBA to OP during winter months but decreased from MBA to OP during summer months, whereas the depth of the canopy SL increased from MBA to OP throughout the study.

The linear relationships between bi-weekly maximum D_H and the surface SL and overall SL at MBA and OP were similar to those observed for canopy SL (Table IIIa; Figures 8b and 10c). The positive correlation between D_H and depth of the surface SL was better at OP than MBA. The positive correlation between D_H and depth of the overall SL was also better at OP than MBA, although these relationships were not as good as those for surface SL. As observed during the photo study for the canopy SL, deeper surface SL and overall SL depths estimated during the field study occurred during periods of large D_H at both sites, and therefore during periods of high storm activity.

Differences in the depth of the surface SL and subsurface SL varied among sites and dates (three-way ANOVA; significant Canopy x Site x Date interaction, F = 1.66, df = 30, 864, p = 0.0154; Figure 11). The depth of the surface SL was significantly

deeper than the depth of the subsurface SL during many of the winter months (Figure 11). Plants that made up the subsurface SL during the winter months had large holdfasts and many broken fronds < 1 m long, indicating they were adult plants that had lost canopy rather than recruits that had not yet grown sufficiently to form a canopy. Giant kelp recruits (small holdfasts, few fronds, few dichotomies, and no surface canopy), however, accounted for much of the subsurface SL during April, May, and June 1994, and April 1995.

The average number of fronds per plant (frond density) for surface SL plants varied only among dates (Table IVa; Figure 12a). Frond density was lowest during winter months and highest during summer months. Multiple comparisons indicate that frond density significantly increased between June and July 1994, and significantly decreased between December 1994 and February 1995. These fluctuations coincided with periods of minimum and maximum D_H, respectively. Frond density for overall SL varied among dates and sites and a site x date interaction was observed for subsurface SL plants (Table IVb-c; Figures 12b-c). Frond density was also lowest during winter months and highest during summer months for overall SL plants, but was highest during winter months and lowest during summer months for subsurface SL plants. Low power, however, hindered the detection of significant differences with multiple comparisons.

Natural fluctuations in algal turf assemblages

A total of 38 species of algae and one species of surfgrass were observed within the study sites between September 1994 and April 1995 (Appendix 2A). Of the 38 species of algae, 24 were categorized as perennial foliose red algae (foliose algae), 4 were categorized as transient red algae (transient algae), and 1 was categorized as an obligate epiphyte, based on previous literature (Foster, 1975; Abbott and Hollenberg, 1976) and results from this study (Appendix 5B). Transient algae were short-lived

species that recruited only after the appearance of bare substrate, whereas perennial foliose red algae did not exhibit such recruitment limitations. Four species of geniculate coralline algae and 8 species of brown algae were also observed. Green algae were not observed during this study. Small red filamentous algae were observed among the holdfasts of turf algae but were rare and, due to difficulties with field identification, they were not recorded. Giant kelp was never recorded within the sampling units and was categorized as rare throughout the study.

Many spatial and temporal patterns were apparent within the algal turf assemblage. Foliose algae dominated the MBA site, geniculate coralline algae dominated the OP site, and the LP site supported a mix of these two groups (Table V; Figure 13). The trend of decreasing foliose algal cover and increasing geniculate coralline cover from MBA to OP was significant throughout the study (non-significant Site x Date interaction; Table V). When examined at the species/genus level, this trend also held for the dominant taxa (Appendices 3A and 4A).

The percent cover of bare substrate was similar among the three sites during September 1994 and April 1995 (Figure 13). It increased from MBA to OP during November 1994 and January 1995, although this trend was not significant (Table V). In contrast, cover of sand was highest at MBA and lowest at OP throughout the study (Figure 6).

Foliose algae exhibited significant temporal variation, decreasing in percent cover from September 1994 to November 1994 following the first major storms of the winter (Table V; Figures 10c and 13). This decrease appeared to be due to a significant decrease in the percent cover of *Gigartina* spp. which dominated the foliose algal assemblages at each site during September 1994 (Appendices 3A and 4A). The percent cover of foliose algae also significantly increased from January 1995 to April 1995, but this increase was not significant for individual taxa. Significant temporal trends were

not observed for geniculate coralline algae (Table V; Figure 13); a significant decrease in percent cover was observed for *Calliarthron tuberculosum*, but not for *C. cheilosporioides* (Appendices 3A and 4A). However, it was hard to distinguish between these two species in the field, and the taxonomic character used for discriminating the species (i.e. the presence of winged intergenicula, *C. cheilosporioides*, vs. cylindrical intergenicula, *C. tuberculosum*) may be a phenotypic response to wave exposure.

Date had a strong effect on the availability of bare substrate (Table V; Figure 13). The percent cover of bare substrate significantly increased from September 1994 to November 1994 and significantly decreased from January 1995 to April 1995 at each site. Although not significant, the percent cover of bare substrate also increased from November 1994 to January 1995 at each site. Sand decreased in percent cover from September 1994 to January 1995; however, this decrease was only significant at LP from September 1994 to November 1994 (Figure 6).

Natural fluctuations in herbivore assemblages

Few species were observed within the herbivore assemblages at the study sites. Of the 8 species observed, only 5 actually occurred within the quadrats (Appendix 2B), and only one, *Tegula* sp., was abundant (Appendix 3B). Spatial and temporal patterns were not apparent for the herbivore assemblage, but a decreasing temporal trend was significant (Table V; Figure 13). This was due to *Tegula* sp., which significantly decreased in density between September 1994 and November 1994 (Appendices 3B and 4B). Temporal trends were not significant for the other species, and the patchy distribution of the kelp crab, *Pugettia producta*, and the lined chiton, *Tonicella lineata*, made statistical analyses inappropriate (Appendices 3B and 4B).

Recruitment to clearings

Giant kelp recruits were observed in the clearings at each site after 92 days (Figure 14), but never in the control plots. Recruits were only observed at MBA on day 92, but recruits were observed on days 141 and 192 at LP and OP. Excluding the two sampling dates at MBA when no recruits were observed, the density of recruits was not significantly different among the seven remaining recruitment events (one-way ANOVA; $F = 0.96$, $df = 6$, $p > .45$). The substrate near all recruits was marked and the recruits were followed until their death. Recruits observed on different days were the result of new recruitment in all cases except two plants, one each from LP and OP, that were first observed on day 141, grew to adult size, and became reproductive.

All recruits observed on day 92 were removed by herbivores at all sites by day 141 as indicated by qualitative observations of blade damage and direct observations of grazing. Herbivore densities peaked in clearings at all sites on day 92 (Sept. 1994; Figure 15), the date corresponding with significantly higher herbivore densities described previously. However, this peak was due to different species at the different sites. A high density of bat stars, *Asterina miniata*, in the clearings at MBA and LP were the cause of the elevated herbivore densities at these sites (Appendix 5A). Densities of bat stars were greater than 2 individuals/0.25 m^2 in the clearings at MBA and LP on day 92, but less than 0.5 individuals/0.25 m^2 at OP during the same period. A peak in *Calliostoma* sp. densities at LP contributed to the high herbivore densities in the clearings at this site. Lined chitons, *Tonicella lineata*, were the only herbivores more abundant in the clearings vs. the control plots at OP on day 92. Removal by water motion, not grazing, was the apparent cause of death for giant kelp recruits observed on days 141 and 192.

Recovery of the turf assemblages varied among the three sites (Figure 15). The lack of independence between subsequent sampling dates would require the use of

Repeated Measures ANOVA to test for site, date, and treatment effects. Multiple comparisons necessary to analyze the recovery process, however, are problematic for Repeated Measures ANOVA (SYSTAT, 1992; von Ende, 1993). Consequently, recovery was qualitatively determined as the point at which the average percent cover of an algal group in cleared plots was within 1 SE of the average percent cover of that algal group in the control plots.

Recovery was faster at MBA than at LP and OP (Figure 15). On day 141, after the presumed grazing event, little bare substrate was available for giant kelp recruitment to the clearings at MBA. Ample substrate, however, was available on days 141 and 192 at LP and OP. Recovery of bare substrate at these sites appeared to occur by day 256. However, this recovery was due to increased percent cover of bare substrate in control plots rather than decreased percent cover of bare substrate in the clearings. If recovery is redefined as the point when clearings reached levels similar to control plots on day 0, then LP clearings did not recover bare substrate until day 345, and OP cleared plots had yet to completely recover by the end of the study. Under this new definition of recovery, recovery of the clearings at MBA was still evident by day 141.

The recovery of bare substrate at each site was due primarily to the growth and recruitment of foliose algae (Figure 15; Appendix 5B). Foliose algae recovered by day 92 at MBA, and by day 192 at LP and OP. However, the percent cover of foliose algae, at the time of recovery, decreased in the clearings from MBA to OP. Geniculate coralline algae recovered slowly at all sites, and did not recover at MBA and OP by the end of the study (Figure 15). They appeared to recover at LP by day 256, but the similarity between clearings and control plots was due to disturbance of control plots rather than recovery of clearings. The higher percent cover of these plants in control plots vs. clearings on day 345 at LP indicates that recovery was not complete. The

percent cover of geniculate coralline algae in control plots on day 0 increased from MBA to OP, as it did based on random sampling of unmanipulated areas (see above).

Irradiance

Average density of germinated giant kelp spores was significantly higher under low irradiance (56.9 ± 1.5/0.16 mm^2; ± SE, n = 4) treatments than under mid irradiance (47.4 ± 0.7), high irradiance (46.7 ± 1.0), and control (46.0 ± 1.3) treatments in the laboratory, and densities under the mid irradiance, high irradiance, and control treatments were not significantly different from each other (one-way ANOVA; $F = 19.41$, $df = 3, 12$, $p < 0.0001$; multiple comparisons, low > mid = high = control). Spores that settled under high irradiance and control treatments did germinate, but began to lose pigment 36 hours after inoculation. Spores under low irradiance and mid irradiance had highly pigmented cytoplasm.

Gametophytes and embryonic sporophytes did not grow to macroscopic size when transplanted to the high irradiance and control treatments in Monterey Harbor. One cm tall sporophytes were, however, observed on substrate that was inoculated with gametophytes (after 3 weeks; 2.0 ± 0.6 sporophytes/25 cm^2; ± SE, n = 3) and embryonic sporophytes (after 2 weeks; 3.0 ± 1.3 sporophytes/25 cm^2; ± SE, n = 3) and placed under the low irradiance treatments. The short time between transplantation and observation of visible sporophytes indicates that the sporophytes were from laboratory inoculations and not natural recruitment. Natural giant kelp recruitment to bare substrate was not observed under any of the treatments after 8 weeks.

Of the four abiotic factors measured during the transplant experiment in Stillwater Cove, only maximum irradiance (i.e. values for the day with highest surface irradiance) had a strong trend with depth (decrease with increasing depth at both sites;

Figure 16). Extinction coefficients (Pickard and Emery, 1982) were calculated at each depth at each site using

$$K = \frac{\ln\left(E_z / E_0\right)}{z},$$

where K = diffuse attenuation coefficient, z = depth, E_0 = irradiance at surface and E_z = irradiance at depth z. Diffuse attenuation coefficients averaged across all depths were similar between the two sites (Site 1, $K = .25$; Site 2, $K = .23$). Temperature and salinity were similar at both sites, and water motion was higher at Site 1 than at Site 2 during the study (Figure 16).

Giant kelp sporophytes were observed on the transplant ropes at both sites (Figure 16). Sporophytes on the embryonic sporophyte treatment at Site 1 grew to macroscopic size after 4 weeks, but only below 3 m depth at a maximum irradiance of 845 $\mu E\ m^{-2}\ s^{-1}$ (Figure 16). Sporophyte density increased with increasing depth from 0.6 ± 0.3 recruits/rope at 3 m to 9.6 ± 8.7 recruits/rope at 7 m. Sporophytes on the gametophyte treatments grew to macroscopic size after 6 weeks, but only at depths greater than 4 m at Site 1 and 5 m at Site 2. This corresponded with maximum irradiances of 750 and 650 $\mu E\ m^{-2}\ s^{-1}$, respectively. Sporophyte densities on the gametophyte treatment were similar among increasing depth at both sites. Natural recruitment was observed after 8 weeks and was also limited to depths greater than 3 m at both sites. Recruit density appeared similar with increasing depth at both sites.

Grazing appeared to be minimal. A few gastropods (*Calliostoma canaliculatum* and *Tegula brunnea*) were observed along the ropes throughout the study, but giant kelp recruits showed no signs of grazing. Moreover, the distribution of grazers was not skewed towards shallower depths, as would be expected if grazing was responsible for the observed sporophyte distributions. The sporophyte and gametophyte treatments were sampled prior to the observed recruitment of other algal species to the lines.

Natural recruitment to the control ropes may have been affected by massive recruitment of benthic diatoms and filamentous brown algae above 3 m depth during the last week of the study. Unidentified hydroids dominated the upper 2 m of one buoy line after the seventh week.

DISCUSSION

Studies of the effects of wave exposure on the structure of intertidal and subtidal algal communities have often focused on putative 'foundation species', species disproportionately important to community maintenance (Dayton, 1972). Experimental manipulation of wave exposure levels, however, is difficult if not impossible, and investigators have been unable to test the causal effect of wave exposure on the distribution of these 'foundation species' (Underwood, 1990; Eberhardt and Thomas, 1991). In the absence of field experiments, transplants and field sampling may provide the most rigorous tests of hypotheses, and most prior research on the effects of wave exposure on kelp has used field sampling or natural experiments (Barrales and Lobban, 1975; Foster, 1982; Dayton et al., 1984; Dayton, 1985; Harrold et al., 1988; Graham et al., in prep.).

Most sampling studies designed to test the effect of wave exposure on algal distribution have qualitatively designated wave exposure levels to the sampling sites (Barrales and Lobban, 1975; Foster, 1982; Dayton et al., 1984; Dayton, 1985). Sites are usually chosen to represent extremes in wave exposure in order to provide for more powerful hypothesis testing. The assumption is that wave exposure is the only abiotic/biotic factor which varies among the sites and, therefore, is the sole factor regulating any among-site differences in the dependent variable(s). There are two problems with this assumption: first, qualitative designations of wave exposure are often vague or inconsistent, resulting in biased level identification; second, without quantifying among-site patterns or identifying correlations between wave exposure and other abiotic/biotic factors, it is difficult to identify which factors, if any, are responsible for observed distribution patterns. Field sampling studies that qualitatively designate

wave exposure levels may only provide weak inferences about the effect of wave exposure on algal distribution (Eberhardt and Thomas, 1991).

I quantified among-site differences in many of the abiotic/biotic factors known to affect giant kelp distributions. Significantly different wave exposures were observed at the three sites (OP, LP, and MBA), and wave exposure was not confounded by other factors that I measured. Bottom temperature varied little between the two extremes of the gradient (i.e. MBA and OP) and did not reach levels known to be detrimental to giant kelp. Nutrient levels were not measured, but the well-mixed nature of the shallow water environment and the positive correlation between temperature and nutrient levels described for central California waters (Traganza et al., 1981) suggests there was little nutrient variation among sites. Similarly, the wave exposure gradient was not confounded by among-site differences in substrate heterogeneity, sand cover, or grazer density. Therefore, among-site differences increasing or decreasing along the gradient were most likely the result of wave exposure rather than any of the other abiotic/biotic factors described above.

Shallow water distribution of giant kelp relative to wave exposure

Wave exposure appeared to regulate temporal variability in the depth of the shallow limit of giant kelp along the Monterey Peninsula. The seasonal trends in depths of the canopy SL, surface SL, and overall SL were significant at OP, LP, and MBA, and significantly correlated with wave exposure at OP and MBA (Tables I and III; Figures 8 and 10). This is similar to the results of Kimura and Foster (1984) who documented seasonal fluctuations in percent cover of giant kelp canopies in a central California kelp forest associated with winter storms. North et al. (1993) also showed that year to year variation in southern California giant kelp canopies often coincided with stormy years.

Seymour et al. (1989) suggested that storm-related mortality of giant kelp plants in a southern California kelp forest regulated the depth of their shallow limit by a combination of entanglement with drifting plants and breaking waves. Drifting plants were rarely seen shallower than 8 m at my sites and entanglement of attached plants with drifting plants was even rarer. This was most likely due to decreasing density of adult plants with decreasing depth (Figure 7 in Harrold et al., 1988; pers. obs.). Entanglement may have occurred but was not directly observed, but the high sampling frequency makes this unlikely. Direct removal of giant kelp plants by water motion, rather than entanglement with drifting plants, appeared to be the most important factor regulating the shallow limit.

Wave exposure appears to regulate the depth of the shallow limit of giant kelp, but ~ 60% of the temporal variability in the depth of the canopy SL, surface SL, and overall SL remained unexplained. This unexplained variability may be due to size-specific mortality of giant kelp. The greatest change in the depth of the canopy SL, surface SL, and overall SL often occurred just after the first winter storms (Figures 8 and 10). The magnitude of wave exposure during these storms was often less than that during subsequent storms, and changes in the depth of the canopy SL, surface SL, and overall SL after the first winter storms were rarely proportional to changes in the magnitude of wave exposure. This is similar to the results of Gerard (1976) and suggests that giant kelp plants were most vulnerable to initial increases in wave exposure.

Observations of average frond density support this hypothesis. Average frond density of surface SL plants and overall SL plants decreased following storms in late December 1993 and November 1994 (i.e. first winter storms), whereas average frond density of subsurface SL plants increased during this period (Figure 12). This increase in frond density of subsurface plants may indicate that some surface plants became

subsurface plants due to the removal of surface canopies, and coincided with increases in the depth of surface SL and overall SL plants (Figure 10).

During periods of low water motion, biomass of giant kelp plants increases drastically due to the growth and initiation of new fronds (Gerard, 1976). Increases in holdfast diameter may be less rapid as production is used for canopy growth (McCleneghan and Houk, 1985). Consequently, drag due to surface canopy biomass may exceed tensile strength of stipes or attachment strength of holdfasts, resulting in the high losses of fronds and entire plants with initial increases in wave exposure. If the drag of giant kelp plants that survive frond losses is reduced below the level of holdfast attachment strength, these plants may be better able to survive periods of increased wave exposure. This is suggested by the significantly shallower depths of the subsurface SL relative to the surface SL (Figure 11). Transplant and tagging experiments are necessary to further test this hypothesis.

Giant kelp plants that lost all of their fronds but retained portions of their basal dichotomies appeared healthy throughout periods of high water motion. These plants were observed to continuously produce fronds that were subsequently removed, presumably by water motion. Much of the decrease in depth of the surface SL and overall SL, during spring and summer, was probably due to a combination of regrowth of subsurface SL plants and sporophyte recruitment.

Some of the unexplained temporal variability in the depth of the surface SL and overall SL might also be explained by processes affecting giant kelp distribution during periods of low water motion. Wave exposure will obviously have little predictive power in explaining temporal fluctuations in giant kelp distributions due to variable growth rates, grazing, or competition. Therefore, the relationship between wave exposure and the depth of the shallow limit probably suffered from the inclusion of data from periods

of low water motion. The removal of such data, however, is highly subjective and was not attempted.

Wave exposure also appeared to regulate spatial variability in the depth of the shallow limit of giant kelp along the Monterey Peninsula. The depths of the canopy SL, surface SL, and overall SL significantly increased from MBA to OP during periods of high water motion. As previously discussed, the only factor documented to be detrimental to giant kelp plants that significantly increased in severity from MBA to OP was wave exposure. Therefore, increased wave exposure at OP most likely caused greater mortality of giant kelp plants, resulting in increased shallow limit depths from MBA to OP during periods of high water motion. This may explain the abrupt northern limit of giant kelp in the Northern Hemisphere: disturbance from more frequent large waves north of Año Nuevo Island (Coastal Data Information Program, 1985-1995) may inhibit the establishment of giant kelp populations as suggested by Foster and Schiel (1985).

Differences were observed between the Site x Date interactions in the depth of the canopy SL, and the surface SL and overall SL. The depth of the canopy SL fluctuated seasonally, but always increased from MBA to OP (Figure 8). The depth of the surface SL and overall SL increased from MBA to OP only during periods of high water motion and decreased during periods of low water motion (Figure 10). This appears to be due to among-site differences in the depth distribution of algal turf assemblages.

Effect of algal turfs on the shallow water distribution and recruitment of giant kelp

The algal turf clearing experiment demonstrated that dense algal turfs inhibit the recruitment of giant kelp in shallow subtidal regions. Giant kelp could not recruit to primary substrate in areas dominated by turfing algae, and plants that recruited as

epiphytes did not survive. Chapman (1984), Dayton et al. (1984), Reed and Foster (1984), and Kennelly and Underwood (1993) observed similar kelp-turf interactions in various subtidal kelp communities (*Laminaria* spp., giant kelp, and *Ecklonia radiata*, respectively) in deeper water than this study. Similarly, Santelices and Ojeda (1984) and Dayton (1985) showed that recruitment of giant kelp could also be inhibited by dense, low intertidal bands of other kelp species (*Lessonia vadosa* and *Durvillaea antarctica*, respectively). The inhibition of giant kelp recruitment at OP, LP, and MBA, as well as those studies mentioned above, was most likely due to reduced light and space under the algal turf assemblages. Kennelly (1987), however, found that *Ecklonia radiata* was unable to recruit to clearings within an Australian turf assemblage, and suggested that allelopathic effects by Dictyotalean algae may have been responsible.

Dense algal turf assemblages are characteristic of shallow subtidal environments along the Monterey Peninsula (Harrold et al., 1988; pers. obs.) and the rest of the California coast (Wells, 1983; Foster and Schiel, 1985; Foster and Schiel, 1992), and tend to decrease in abundance with depth (Aleem, 1973; Devinny and Kirkwood, 1974; Barrales and Lobban, 1975; Womersley, 1981; Harrold et al., 1988; pers. obs.). Thus, the growth of most giant kelp plants (i.e. those plants that make up the continuous giant kelp surface canopy; Figure 2) was probably limited to the region where turf algae begin to decrease and bare substrate becomes more available. This region tended to be in increasingly deeper water from MBA to OP, and the depth of the canopy SL significantly increased from MBA to OP. Plants that were able to recruit to areas where the algal turfs were disturbed contributed to the "shallowing" of the surface SL and overall SL depths at each site during periods of low water motion. Consequently, as potential for recruitment to shallow water appeared to increase from MBA to OP, the depth of the surface SL and overall SL decreased from MBA to OP. Therefore, wave exposure appears to have directly regulated the canopy SL, surface SL, and overall SL

during periods of high water motion, and indirectly regulated the canopy SL, surface SL, and overall SL during periods of low water motion.

The composition of the algal turf assemblages changed as wave exposure levels varied. Temporal and spatial increases in wave exposure resulted in significant decreases in percent cover of foliose algae but not of geniculate coralline algae. Geniculate coralline algae appear able to survive periods of extreme water motion, recovering bare substrate in the absence of less wave exposure-resistant, but faster-growing, foliose algae. Consequently, the species composition of the algal turf assemblages described during this study may be a result of disturbance-mediated competition for space, most within-site variation being due to fluctuation in the percent cover of foliose algae.

Recovery rates of the algal turf assemblages varied with a change in species composition. The assemblage at MBA (dominated by foliose algae) recovered quickly from disturbances made during late spring 1994. Recovery was slowest at OP (dominated by geniculate coralline algae) with ~ 20% cover of bare substrate available in late April 1995. The delayed recovery of disturbed algal turf assemblages with increasing wave exposure allowed for longer giant kelp recruitment windows at LP and OP relative to MBA. Consequently, giant kelp recruitment at MBA was severely affected by grazing during September 1994. Bare substrate was not available for subsequent giant kelp recruitment at MBA once grazer densities decreased. Giant kelp recruitment, however, continued at LP and OP until December 1994. These additional recruitment events allowed individuals at both LP and OP to reach the surface and become reproductive. Therefore, although the percent cover of bare substrate available for giant kelp recruitment was not significantly different among-sites during early spring 1995 (Table V; Figure 13), and recruit density was not significantly different among-sites (Figure 14), longer recruitment windows with increasing wave exposure probably

resulted in the significantly shallower depth, with increasing wave exposure, of the surface SL and overall SL previously described during periods of low water motion.

Despite increased potential for recruitment of giant kelp to shallow water with increasing wave exposure, the availability of bare substrate for recruitment was low at all sites. Percent cover of bare substrate peaked at ~35% at OP in January 1995, during the most wave exposed period since 1985 (Figures 8 and 10). If percent cover of bare substrate is directly proportional to disturbance by wave exposure, then the percent cover of bare substrate was most likely much lower than 35% during previous years. The few giant kelp plants able to recruit to shallow water probably had little shading effect on the algal turf assemblages, and were probably removed during the first winter storms. This would reinforce the dominance of shallow water regions by turfing algae.

Effect of shallow water light environment on survival of giant kelp microscopic stages

The results of the irradiance manipulations indicated that high irradiance negatively affects the microscopic stages of giant kelp in shallow water. Spore settlement was significantly decreased in high irradiances treatments. The density of germinated spores, however, was still high under high irradiance treatments indicating that high irradiances did not prohibit spore settlement. Transplanted gametophytes and embryonic sporophytes were able to grow to macroscopic size in water shallower than 2 m only if shaded, and mortality of giant kelp microscopic stages decreased with decreasing irradiance levels in vertical transplants on ropes.

The results of the transplant experiments also suggest that vulnerability of microscopic stages to high irradiance decreased with increasing plant development. Sporophytes from gametophyte transplants were observed in lower densities under shade manipulations and in deeper depths along vertical transplant lines than sporophytes from

embryonic sporophyte transplants. Moreover, Anderson (1965) found bleaching of giant kelp juveniles in shallow water, but did not observe 100% mortality. That this pattern was due to longer exposure of gametophytes to grazing pressure was unlikely because grazer densities were low and grazer damage was not observed. However, the effects of micro-grazers could not be determined and may have been substantial.

Wood (1987) demonstrated the lethal effects of high irradiance on *Ecklonia radiata* juveniles through a series of laboratory shading manipulations similar to those conducted on giant kelp during this study, and suggested that UV radiation may regulate the shallow limit of *E. radiata* populations. He observed that UV rather than PAR was responsible for decreased survivorship, decreased photopigment concentrations, and increased UV-absorbing pigment concentrations. In contrast, Lüning (1980) found 50% mortality in *Laminaria hyperborea* gametophytes in the presence of high visible light radiation. Lethal doses at 750 μ E m^{-2} s^{-1} were observed after a few hours. This value is similar to PAR irradiances associated with inhibition of giant kelp recruitment in the field. I conclude that high irradiance determined the absolute shallowest limit of giant kelp in these experiments by killing giant kelp microscopic stages. Without direct UV irradiance values and estimates of critical doses required for giant kelp mortality (i.e. lethal doses); however, it is impossible to determine which spectral component was responsible for the observed mortalities.

Although rare, giant kelp plants with conical holdfasts can be found in intertidal regions in California (North, 1971; M. S. Foster, pers. comm.; pers. obs.). These appear to occur in places with micro- and macro-scale shading of the substrate, or are the result of large plants transported into shallow water on cobbles. Most plants occur under shaded ledges or on the side of pools where irradiance is relatively low but sufficient to support recruitment and growth. Still other plants have been observed to recruit to small boulders, become buoyant enough to float the boulders into shallow water, then

overgrow the boulders, thereby attaining firm attachment to the substrate. These mechanisms allow plants to develop under sub-lethal irradiance conditions to the stage where they are no longer vulnerable to high irradiances. Field observations indicate that this resistance to high irradiance develops prior to the formation of the first primary dichotomy (Anderson, 1965; pers. obs.). Therefore, during extended periods of sub-lethal irradiance levels (e.g. fog, storms, high latitude regions), giant kelp plants may gain access to intertidal regions, if only temporarily.

Conclusions

Much of the regulation of the shallow limit of giant kelp appears to be driven by the direct removal of adult plants by water motion. Individual effects of the various parameters of wave exposure (e.g. D_H, H_S at breaking, BD) could not be determined because these parameters co-vary. Storms generally exhibited large D_H, large H_S at breaking, and deep BD, and all of these parameters were probably important in the removal of giant kelp plants. Giant kelp mortalities were probably also influenced by high onshore winds that coincided with periods of high wave exposure, and biased giant kelp canopies in the onshore direction. Future studies to describe variation in D_H, H_S at breaking, BD, and any other parameters associated with wave exposure, by a single wave exposure index, would be beneficial for modeling wave-induced giant kelp mortality. For the present, I conclude that storms (i.e. high wave exposure and high onshore winds) appeared to regulate directly the shallow limit of giant kelp during periods of high storm activity, at least along the Monterey Peninsula.

Storm activity also appeared to regulate indirectly the shallow limit of giant kelp during periods of low storm activity. Giant kelp is the dominant competitor for light within its distributional range, decreasing light available to underlying algae. In the absence of giant kelp surface canopies, however, algal turf assemblages are the

dominant competitors for space, inhibiting giant kelp recruitment. Therefore, by removing giant kelp surface canopies in shallow subtidal regions, storms allow for the persistence and dominance of algal turf assemblages and the relative exclusion of giant kelp populations from shallow water. In the absence of wave exposure, giant kelp plants that recruit to available bare space or as epiphytes on the turfing algae should be able to survive long enough to negatively affect the underlying algae through shading. This would most likely promote a persistent giant kelp population in the shallow subtidal region, reflected by the decreasing depth of the continuous giant kelp surface canopy from OP to MBA during this study.

The interaction of direct and indirect mechanisms regulating algal distributions in the shallow subtidal region by wave exposure may be best described as disturbance-meditated competition. Algal turf assemblages become dominant competitors for space only if wave-induced mortality of giant kelp is high. In absence of such disturbances, giant kelp dominates the system, as in subtidal regions. Thus, shallow water environments may have different algal compositions depending on the level of disturbance: giant kelp-dominated communities (low disturbance) and algal turf-dominated communities (high disturbance). The continuous nature of the wave exposure regimes along the Monterey Peninsula suggest that an abrupt transition between the two compositions rarely occurs.

Even in total absence of wave-induced mortality and inter-specific competition, giant kelp populations rarely extend into water as shallow as do many other kelp species, or its congener, *Macrocystis integrifolia*. This exclusion from shallow water may be influenced by pollution, grazing, substrate type, or nutrient limitations. The absolute shallowest limit of giant kelp, however, appears to be determined by photo-damage from high irradiance. Total mortality due to high irradiance probably limits survival of giant kelp microscopic stages prior to stresses of desiccation and temperature that commonly

limit the upper distribution of intertidal algae. Therefore, because of the physiological similarities of microscopic stages within the Laminariales (Lüning and Neushul, 1978; Henry and Cole, 1982), high irradiance may be an important unrecognized mechanism structuring intertidal kelp communities.

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Table I. Analysis of variance for depth of (A) canopy SL, (B) surface SL, and (C) overall SL plants.

A. Source of variation	df	ms	F	p
Site	2	301.21	673.63	<0.0001
Date	45	10.67	23.87	<0.0001
S x D	90	2.39	5.35	<0.0001
Error	1242	0.48		

B. Source of variation	df	ms	F	p
Site	2	13.16	1.11	0.333
Date	15	99.13	8.29	<0.0001
S x D	30	24.79	2.08	<0.001
Error	432	11.95		

C. Source of variation	df	ms	F	p
Site	2	1.84	8.26	<0.001
Date	15	5.31	23.85	<0.0001
S x D	30	0.75	3.36	<0.0001
Error	432	0.22		

Table II. Pearson product-moment correlations (r) between abiotic factors at (A) MBA and (B) OP. All data were bi-weekly averages between March 1986 and September 1989. Values greater than 0.5 are highly correlated (n = 39).

		Source of variation			
A.	Source of variation	H_s at breaking	D_H	BD	Wind Vel.
	H_s at break.	1.00	-	-	-
	D_H	0.88	1.00	-	-
	BD	0.96	0.77	1.00	-
	Wind Vel.	0.58	0.68	0.52	1.00

		Source of variation			
B.	Source of variation	H_s at breaking	D_H	BD	Wind Vel.
	H_s at break.	1.00	-	-	-
	D_H	0.96	1.00	-	-
	BD	0.95	0.87	1.00	-
	Wind Vel.	0.62	0.72	0.59	1.00

Table III. Linear regressions of (A) canopy SL, surface SL, overall SL, and subsurface SL (dependent variables) vs. horizontal orbital displacement (D_H; independent variable) at MBA and OP, (B) overall SL (dependent variable) vs. surface SL or subsurface SL (independent variables) at MBA, LP, and OP. Denominator degrees of freedom were: canopy SL, 37 for MBA and 36 for OP; others, 15 for MBA and 14 for OP. NS - not significant.

A. Regression	slope	y-intercept	F	p	r^2
MBA: canopy SL vs D_H	0.37	2.68	26.24	<0.0001	0.415
MBA: surface SL vs D_H	0.45	2.07	6.31	0.024	0.296
MBA: overall SL vs D_H	0.46	2.72	5.35	0.036	0.200
MBA: subsurface SL vs D_H	0.44	2.51	2.04	0.173	NS
OP: canopy SL vs D_H	0.72	3.45	26.99	<0.0001	0.428
OP: surface SL vs D_H	0.72	1.43	7.85	0.014	0.359
OP: overall SL vs D_H	0.82	1.85	6.35	0.025	0.312
OP: subsurface SL vs D_H	0.54	2.19	3.56	0.08	NS

B. Regression	slope	y-intercept	F	p	r^2
MBA: overall SL vs surface SL	0.69	0.43	41.05	<0.0001	0.732
MBA: overall SL vs subsurface SL	0.51	1.22	25.16	0.0002	0.627
LP: overall SL vs surface SL	0.75	0.24	109.94	<0.0001	0.881
LP: overall SL vs subsurface SL	0.53	1.12	11.09	<0.0001	0.425
OP: overall SL vs surface SL	0.76	0.24	95.33	<0.0001	0.872
OP: overall SL vs subsurface SL	0.91	-0.02	66.52	0.0046	0.826

Table IV. Analysis of variance for frond density of (A) surface SL, (B) overall SL, and (C) subsurface SL plants.

A. Source of variation	df	ms	F	p
Site	2	417.71	1.55	0.2135
Date	15	1791.33	6.64	<0.0001
S x D	30	342.81	1.27	0.1569
Error	432	269.58		

B. Source of variation	df	ms	F	p
Site	2	867.53	3.64	0.0270
Date	15	632.71	2.66	<0.001
S x D	30	133.27	0.56	0.9726
Error	432	238.11		

C. Source of variation	df	ms	F	p
Site	2	2.61	5.92	0.0029
Date	15	9.03	20.54	<0.0001
S x D	30	1.22	2.78	<0.0001
Error	432	0.44		

Table V. Analysis of variance for the effect of Site and Date on percent cover of algae, bare substrate, and density of herbivores at MBA, LP, and OP, between September 1994 and May 1995. Contrasts were using Dunn-Sidak corrected alpha values.

	Source of variation			
Category	Site	Date	Site*Date	Contrasts
Foliose algae	F = 57.50; df = 2; P < 0.0001	F = 55.36; df = 3; P < 0.0001	F = 1.59; df = 6; P > 0.15	MBA > LP > OP S > N = J < A
Transient algae	N/A	F = 5.95; df = 3; P < 0.001	N/A	S > N = J = A
Geniculate coralline algae	F = 52.15; df = 2; P < 0.0001	F = 2.61; df = 3; P > 0.05	F = 1.03; df = 6; P > 0.4	MBA < LP < OP
Bare substrate	F = 0.67; df = 2; P > 0.5	F = 21.38; df = 3; P < 0.0001	F = 1.83; df = 6; P > 0.1	S < N = J > A
Herbivores	F = 0.30; df = 2; P > 0.7	F = 7.37; df = 3; P < 0.001	F = 1.97; df = 6; P > 0.05	S > N = J = A

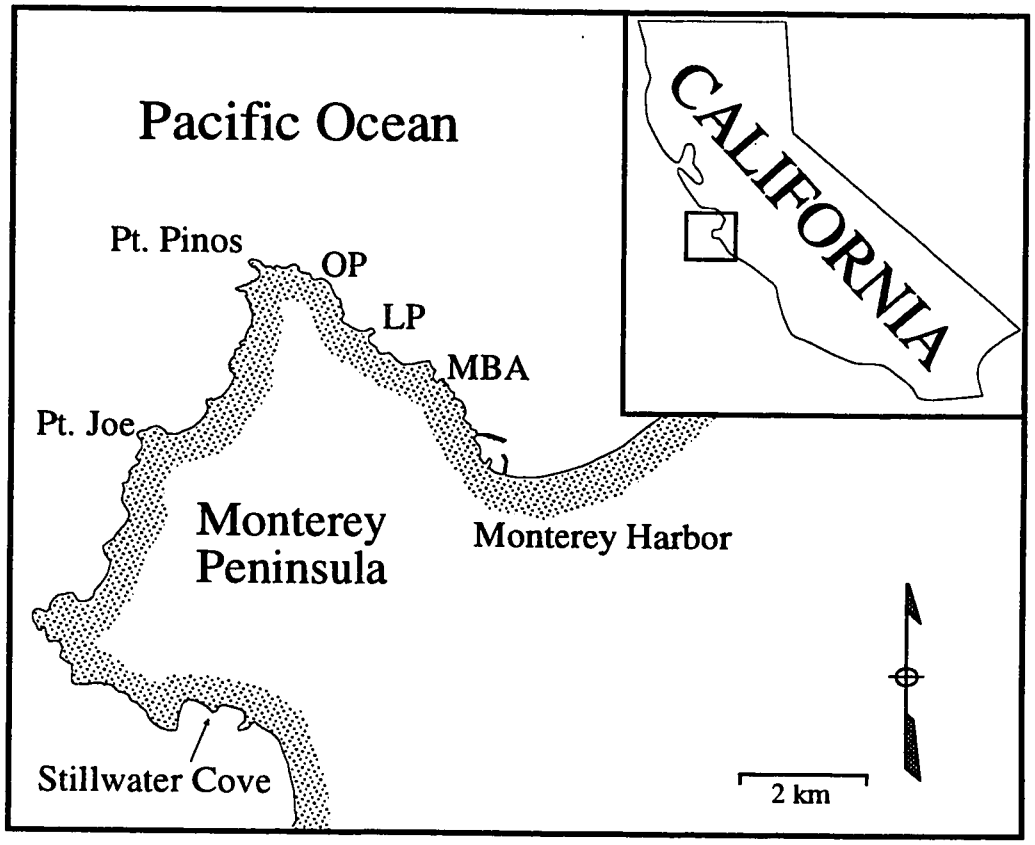


Figure 1. Location of study sites.

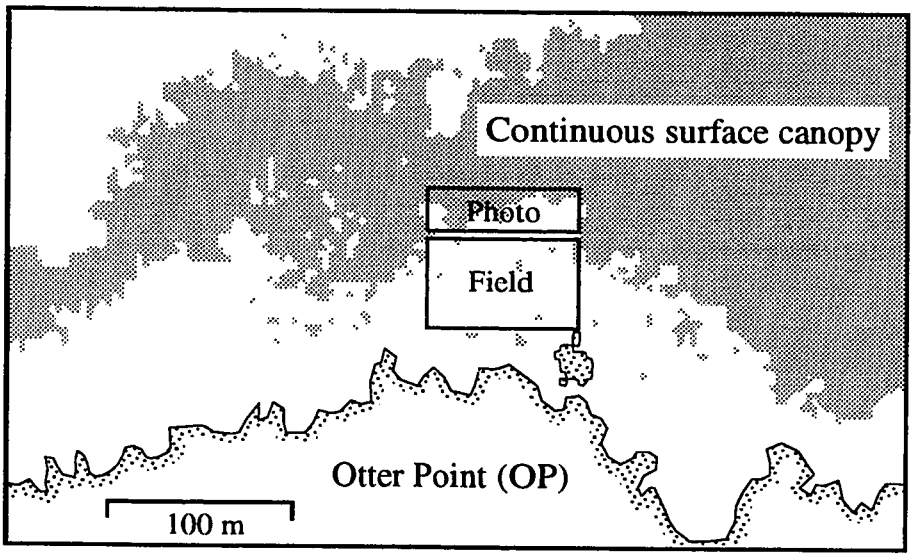


Figure 2. Area surveyed by the photo study and field study at OP. Notice the photo study was along the inner edge of the continuous giant kelp surface canopy, whereas the field study was within the region relatively devoid of giant kelp between the surface canopy and the shore.

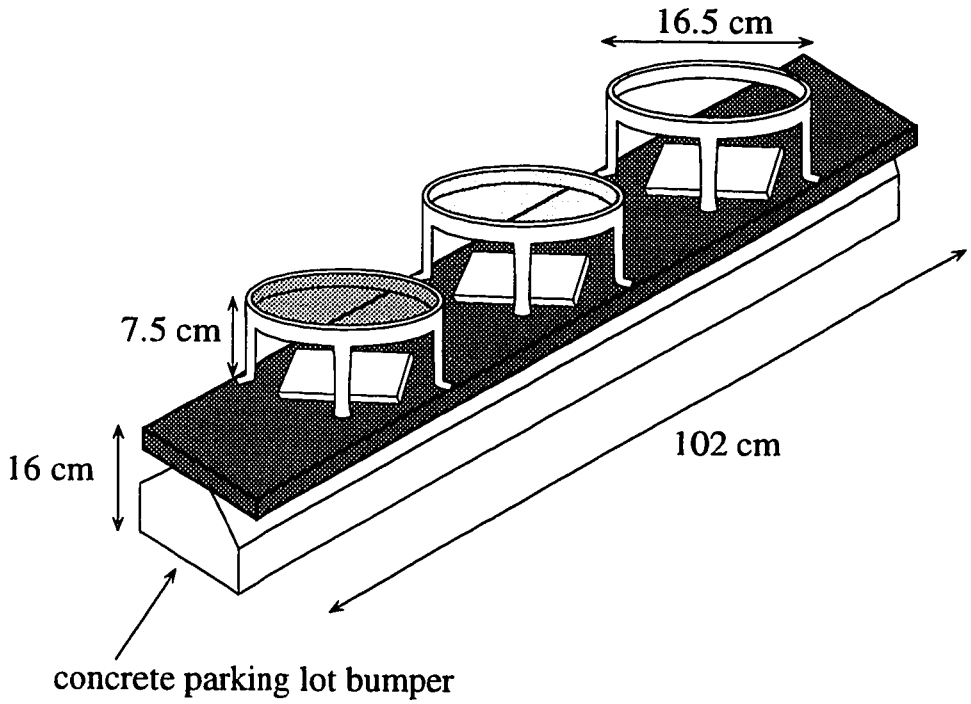


Figure 3. Diagram of a shade manipulation transplant block showing the 3 treatments: low irradiance (▒▒▒ ; PVC frame, 3 mm thick tinted-Plexiglass), high irradiance (▭ ; PVC frame, 3 mm thick untinted-Plexiglass), roof-control (▭ ; PVC frame only). The location of transplant plates (innoculated with giant kelp microscopic stages) is shown under each treatment.

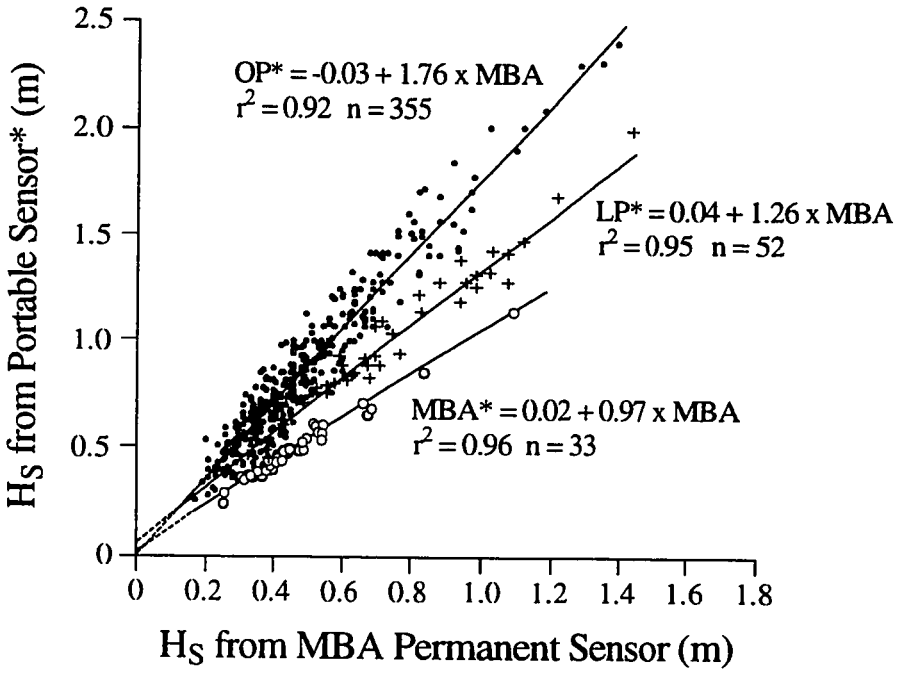


Figure 4. Linear relationship between H_S measured by the permanent sensor at MBA, and H_S measured by the portable sensor placed at MBA (○), LP (+), and OP (●).

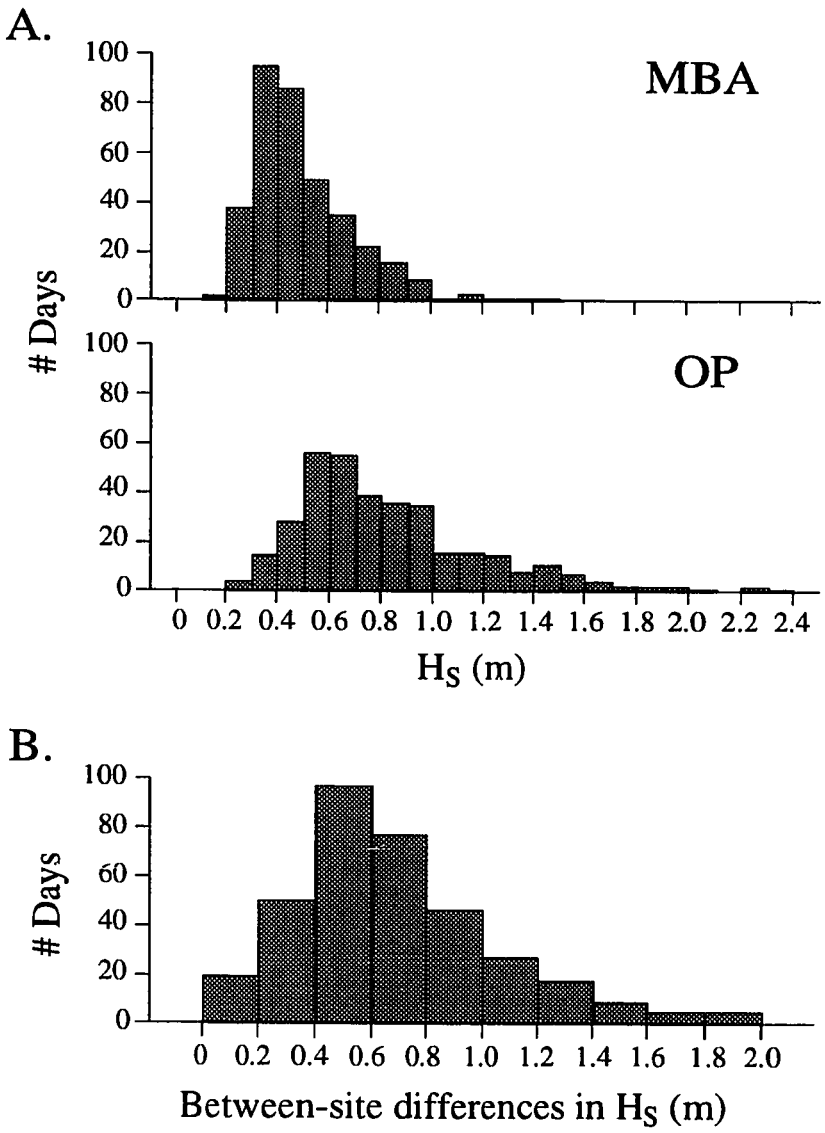


Figure 5. Frequency of occurrence (in days) of (A) H_S estimated at MBA and OP, and (B) differences in H_S between MBA and OP for all days in which H_S was measured at both sites simultaneously. All differences are positive indicating higher H_S estimates at OP, n = 355 for each histogram.

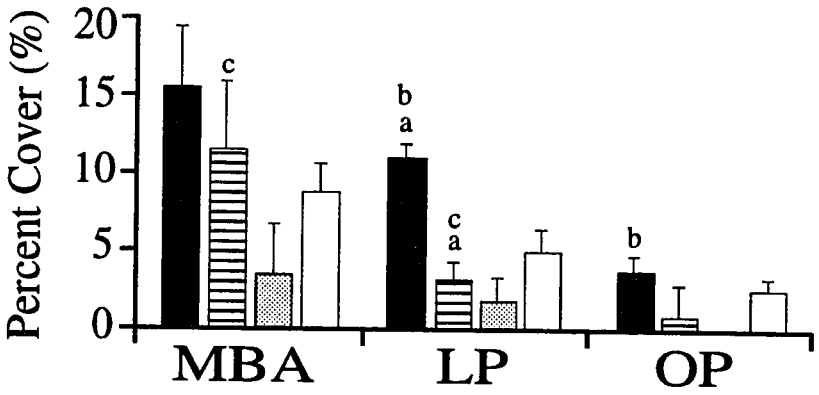


Figure 6. Percent cover of sand at MBA, LP, and OP in Sep 94 (■), Nov 94 (▤), Jan 95 (▩), Apr 95 (□); $\bar{x} \pm$ SE, n = 7; same letters indicate significant differences using Dunn-Sidak contrasts.

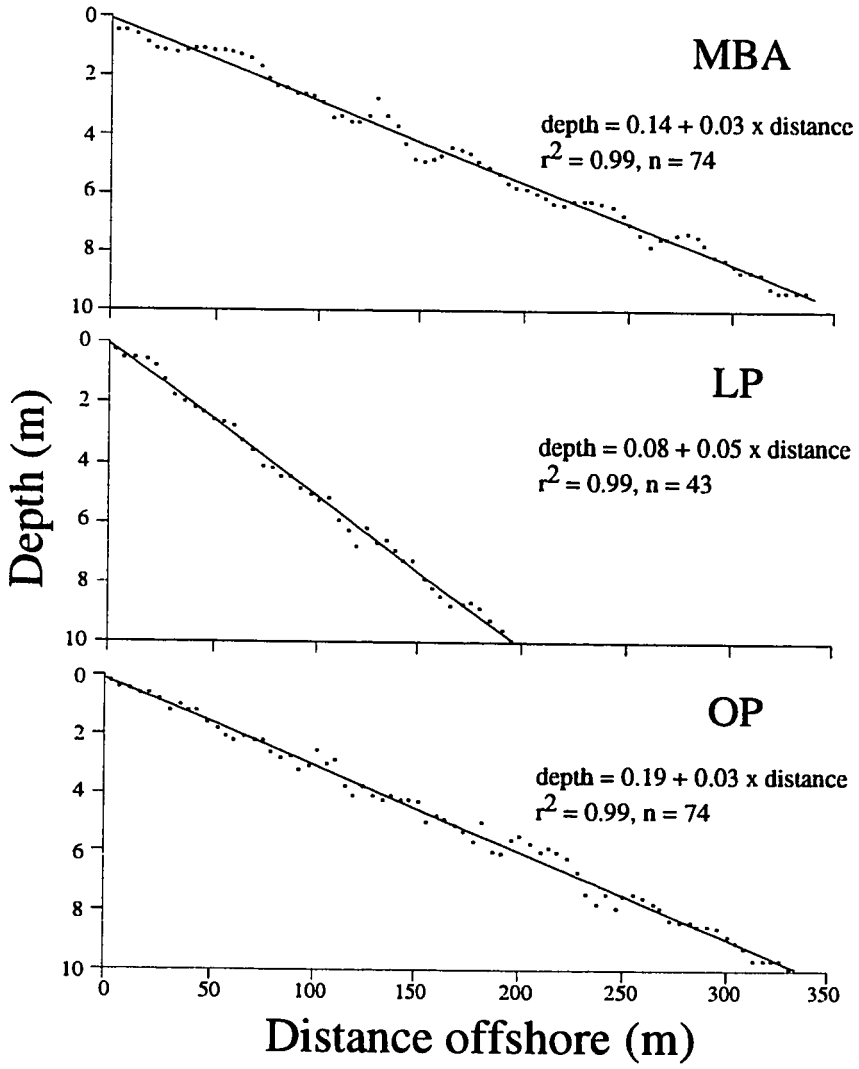


Figure 7. Depth vs distance profiles. Data points represent the average depth at 4.5 m intervals along 3 transects placed perpendicular to shore at each site. Permanent transects were at 45 m at LP and 90 m at MBA and OP.

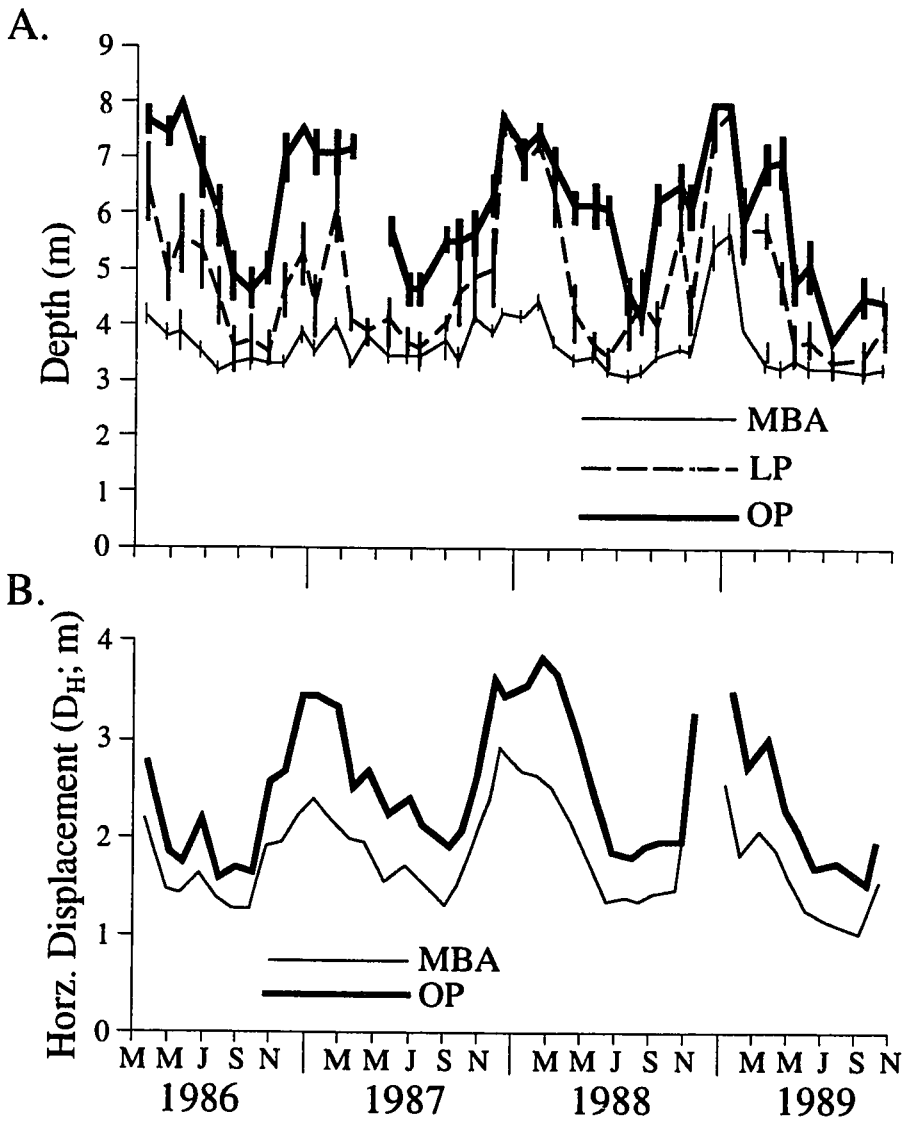


Figure 8. Variability in (A) depth of the canopy SL at MBA, LP, and OP ($\bar{x} \pm$ SE, n = 10), and (B) horizontal orbital displacement (D_H; average for 14 days prior to SL estimates) at MBA and OP, between March 1986 and November 1989.

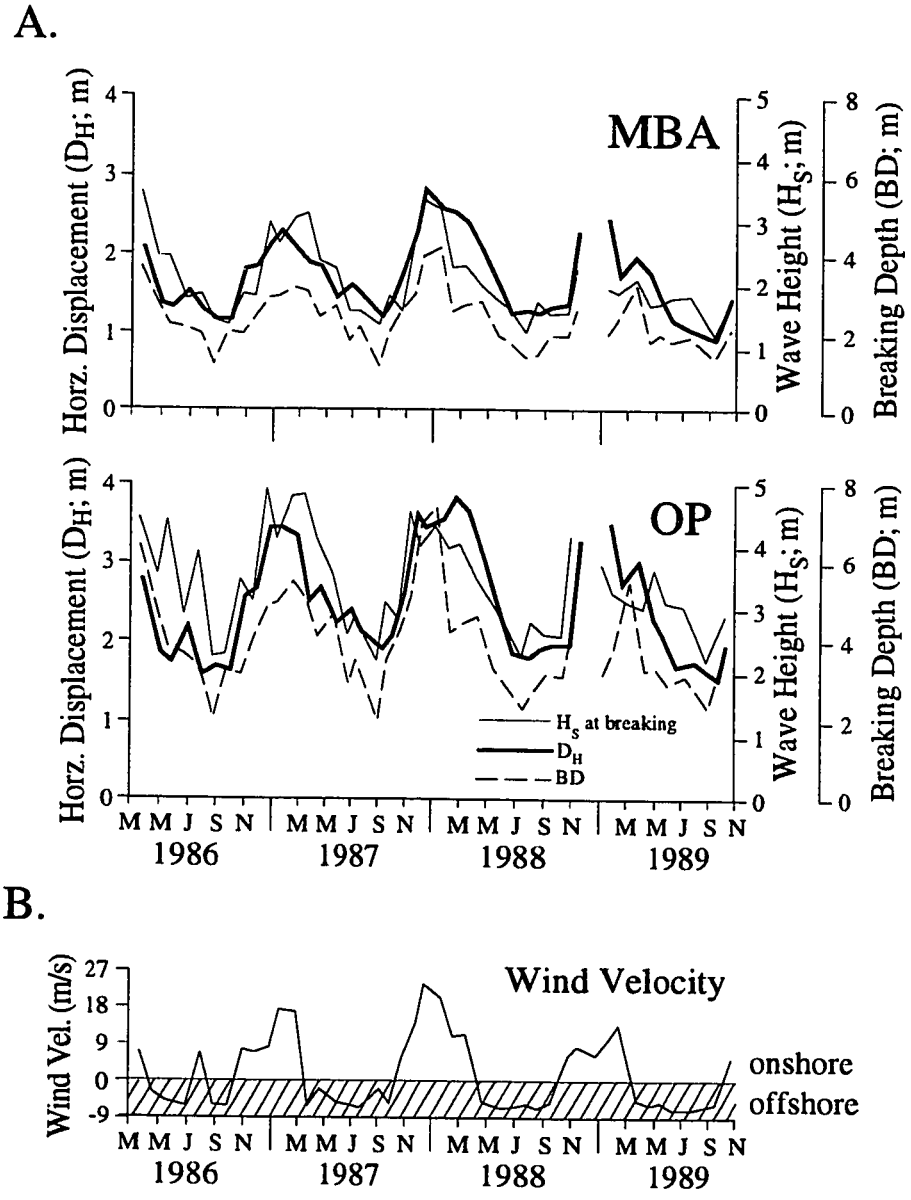


Figure 9. Temporal and spatial variability in (A) wave exposure parameters at MBA and OP, and (B) average daily wind velocity at MBA. Data points are average values for the 14 days prior to each date when canopy SL estimates were made. The hatched region in B) indicates dates of offshore winds. Onshore direction = 40° true.

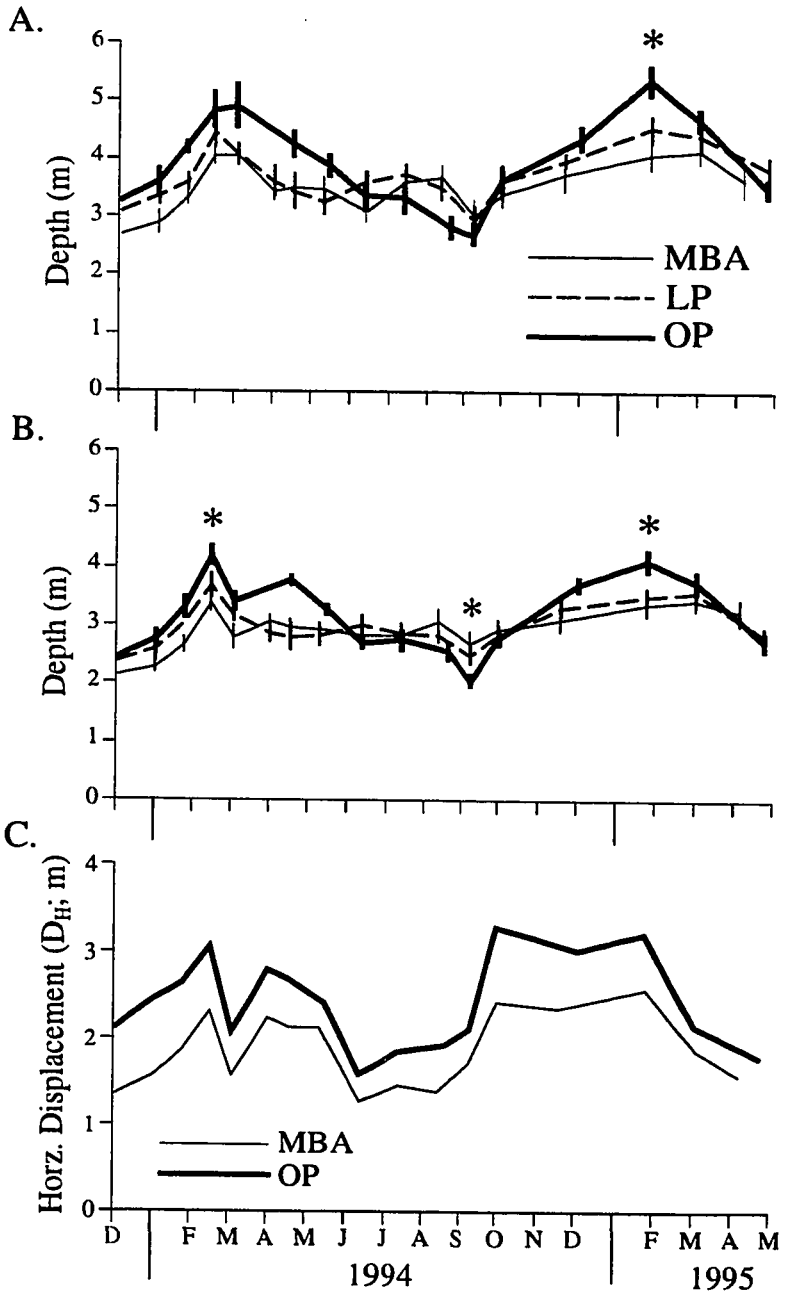


Figure 10. Variability in (A) depth of surface SL and (B) overall SL at MBA, LP, and OP ($\bar{x} \pm SE$, n = 10), and horizontal orbital displacement (D_H; average for 14 days prior to SL estimates) at MBA and OP, between December 1993 and May 1995. Asterisks indicate dates when among-site differences were significant.

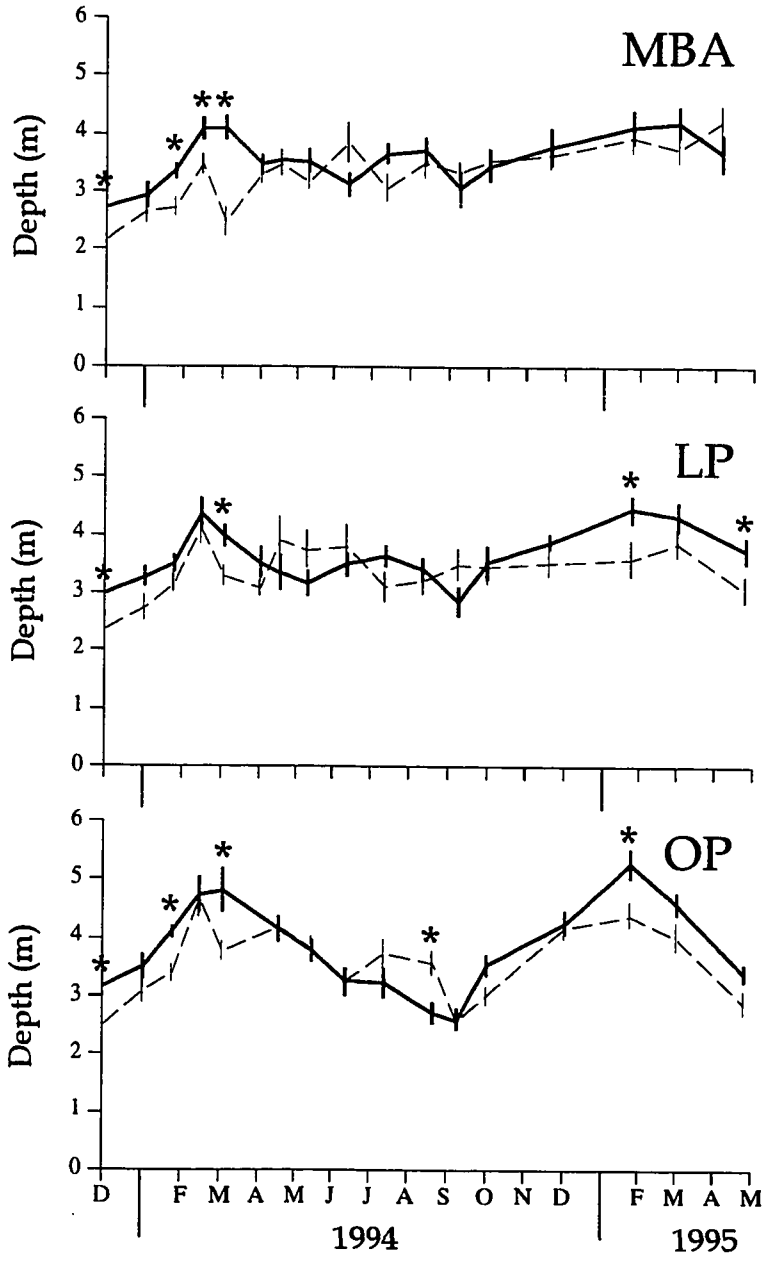


Figure 11. Comparisons between the depth of surface SL (——) and subsurface SL (– – –) at MBA, LP, and OP from December 1993 to May 1995 ($\bar{x} \pm SE$, n = 10). Asterisks indicatedates when surface SL depths vs. subsurface SL depths were significantly different.

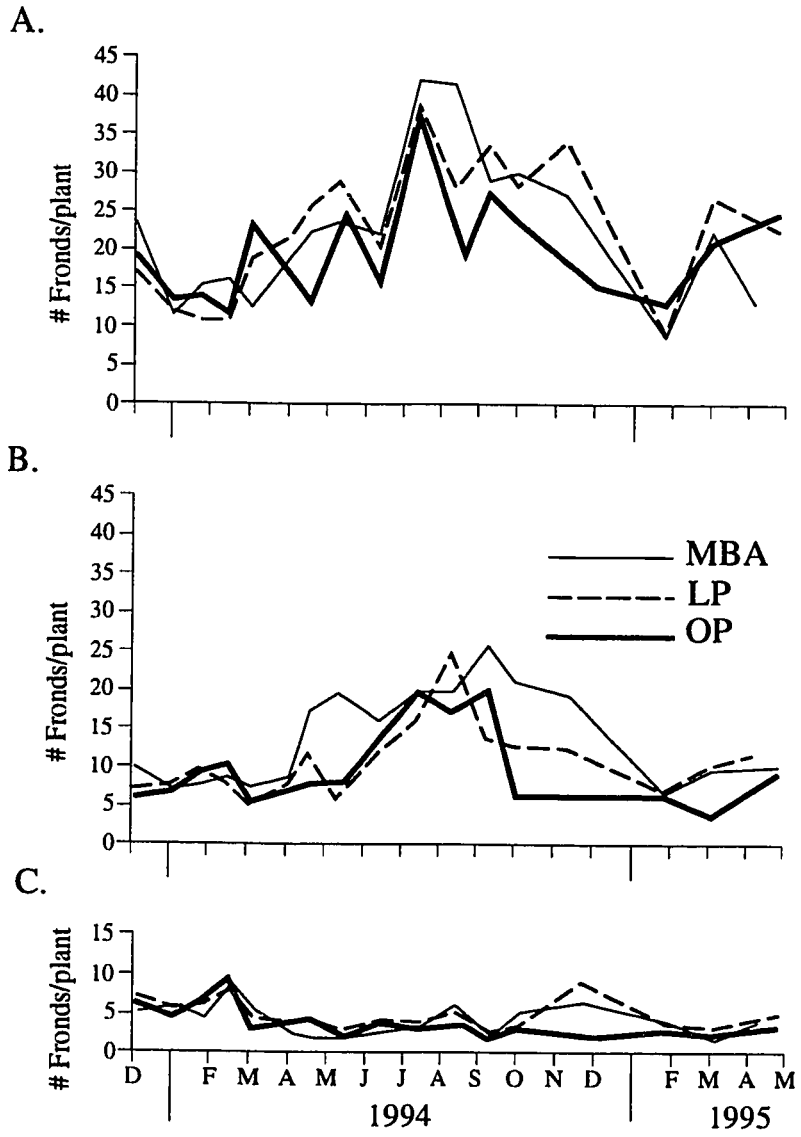


Figure 12. Average number of fronds per plant for (A) the surface SL, (B) the overall SL, and (C) the subsurface SL at MBA, LP, and OP between December 1993 and May 1995. Stipe densities were highly variable at each site; error bars omitted for clarity ($\bar{x}$, n = 10).

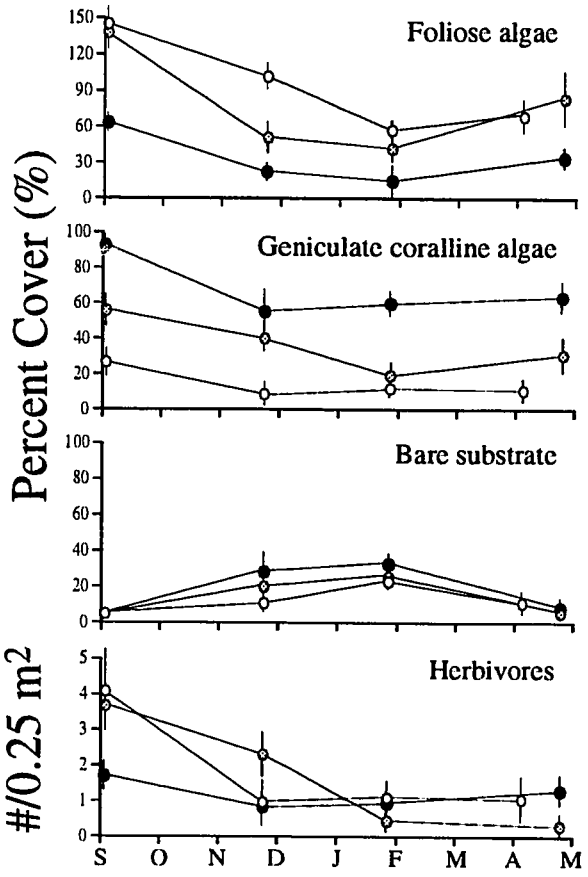


Figure 13. Abundance of organisms at MBA (○), LP (◎), and OP (●) between September 1994 and May 1995 ($\bar{x} \pm$ SE, n = 7). Algae, and bare substrate are expressed as percent covers; herbivores are densities. Note the scale change in the y-axis for foliose algae.

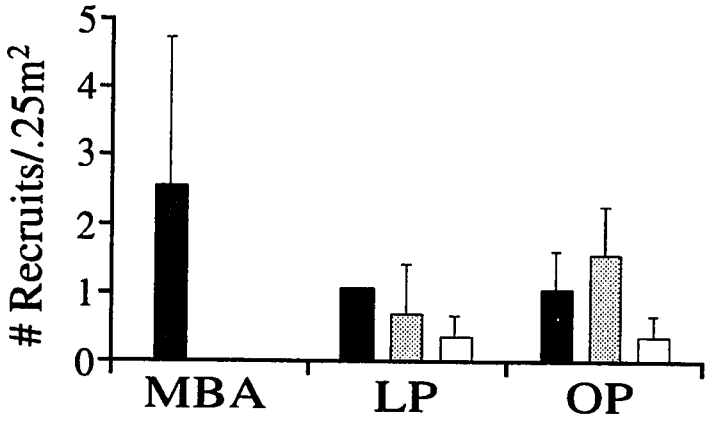


Figure 14. Giant kelp recruitment ($\bar{x} \pm SE$, n = 3) to clearings at each of the three sites on day 92 (■), day 141 (▨), and day 192 (□). No recruitment was observed at MBA after day 92, or at LP and OP after day 192.

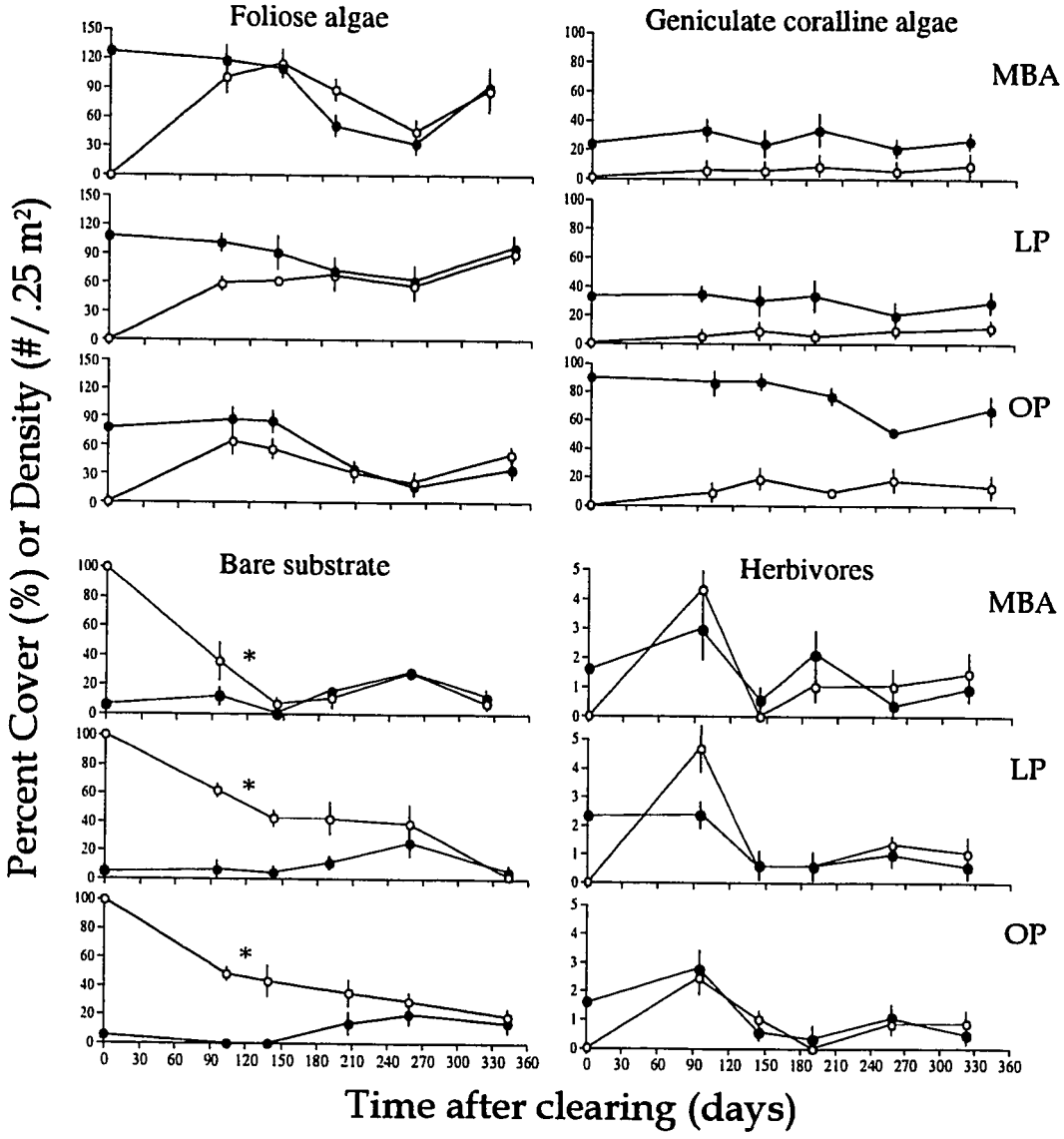


Figure 15. Recovery of turf algae (% cover) and density of herbivores, in clearings (O) and control plots (●) as a function of time after clearing at MBA, LP, and OP ($\bar{x} \pm SE$, n = 3). Asterisks indicate the time of peak herbivore densities

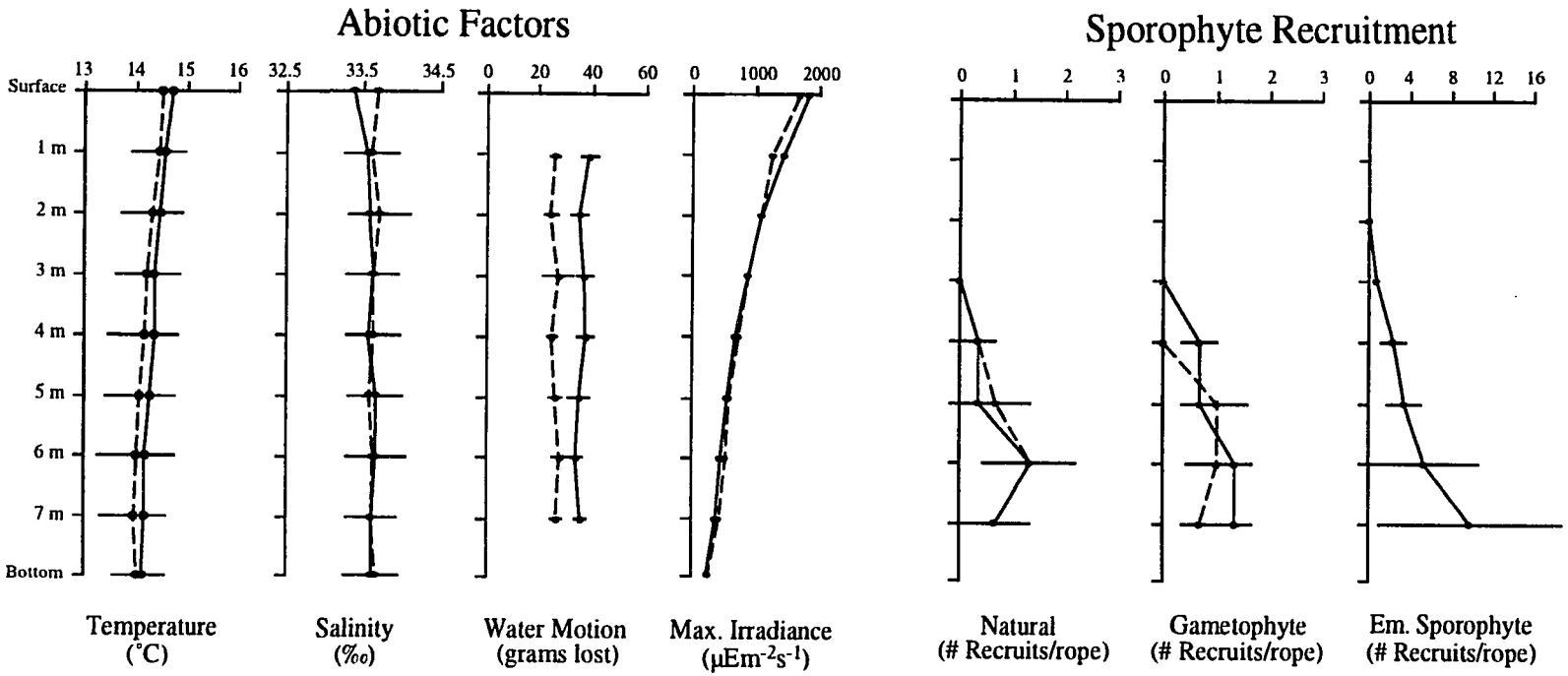


Figure 16. Depth distributions of abiotic factors, and the growth of giant kelp sporophytes to macroscopic size, at Site 1 (———) and Site 2 (– – – –) in Stillwater Cove ($\bar{x} \pm SE$, n = 3, except maximum irradiance).

Appendix 1. General formulae used in wave modelling FORTRAN program.

The wave modelling program estimated energy flux balance by numerically integrating the following equation along a bottom profile:

$$EC_{gx}\big|_2 = EC_{gx}\big|_1 + \langle \varepsilon_b \rangle\big|_1 \Delta x + \langle \varepsilon_f \rangle\big|_1 \Delta x$$

where

$$E = \frac{1}{8}\rho g H_{rms}^2$$

$$C_{gx} = \frac{C}{2}\left(1 + \frac{2kh}{\sinh 2kh}\right)\cos\bar{\theta}$$

$$\langle \varepsilon_b \rangle = \frac{3\sqrt{\pi}}{16}\rho g B^3 \bar{f}\frac{H_{rms}^5}{\gamma^2 h^3}\left[1 - \frac{1}{\left(1 + \left(H_{rms}/\gamma h\right)^2\right)^{5/2}}\right]$$

$$\langle \varepsilon_f \rangle = \rho c_f \frac{1}{16\sqrt{\pi}}\left[\frac{2\pi \bar{f} H_{rms}}{\sinh kh}\right]^3$$

Here, E is energy density, ρ is seawater density, g is gravity, H_{rms} is root mean square wave height. The x component of group velocity is C_{gx}, k is wave number, h is depth, and θ is mean direction. Bore dissipation is denoted by $<\varepsilon_b>$, B is the breaker coefficient (determined internally by the program), f is average frequency, and γ is 0.42. Frictional dissipation is denoted by $<\varepsilon_f>$ and c_f is the bed friction coefficient (0.01).

The result of the model is H_S at breaking, from which maximum D_H (horizontal orbital displacement) is estimated using:

$$D_H = -\left\{\frac{H}{2}\right\}\frac{\cosh(kd)}{\sinh(kd)}$$

Appendix 2. Relative abundance of (A) macroscopic algae, and (B) herbivores, at MBA, LP, and OP. Algae: common - cover > 5% on at least one sampling date; uncommon - cover ≤ 5%; rare - species observed but not contacted by sampling unit; bold print indicates dominant species in a multispecies genus. Herbivores: common - observed within the sampling unit on more than one sampling date; uncommon - observed within the sampling unit on only one sampling date; rare - observed at site but not within the sampling unit.

	Site		
A. Category	MBA	LP	OP
Rhodophyta			
Foliose algae			
Botryocladia pseudodichotoma	common	common	rare
Callophyllis flabellulata	rare	rare	rare
Cryptopleura farlowiana	common	common	common
Fauchea laciniata	rare	rare	rare
Gelidium robustum	uncommon	uncommon	uncommon
G. purpurascens	uncommon	uncommon	uncommon
Gigartina corymbifera	common	common	common
G. exasperata	uncommon	uncommon	uncommon
Gymnogongrus platyphyllus	rare	-	uncommon
Halymenia coccinea	rare	rare	rare
Iridaea cordata var. *splendens*	-	uncommon	rare
Laurencia spectabilis	-	uncommon	-
Microcladia coulteri	common*	common*	common*
Neoptilota densa	uncommon	-	uncommon
Plocamium cartilagineum	uncommon	-	-
Prionitis lanceolata	common	common	common
P. linearis	common	common	common
P. cornea	rare	rare	rare
Rhodymenia californica	common	common	rare
R. pacifica	uncommon	uncommon	rare
Sarcodiotheca gaudichaudi	uncommon	common	common
Transient algae			
Gymnogongrus leptyphyllus	common	common	common
Holmesia californica	rare	uncommon	rare
Pseudogloiphloea confusa	uncommon	uncommon	rare
Rhodoglossum roseum	uncommon	uncommon	uncommon
Geniculate coralline algae			
Bossiella californica var. californica	uncommon	rare	rare
B. orbigiana var. *orbigiana*	-	rare	uncommon
Calliarthron cheilosporoides	common	common	common
C. tuberculosum	common	common	common
Corallina vancouveriensis	uncommon	rare	rare
Non-geniculate coralline algae	common	common	common
Phaeophyta			
Colpomenia peregrina	uncommon	-	-
Cystoseira osmundacea	rare	rare	rare

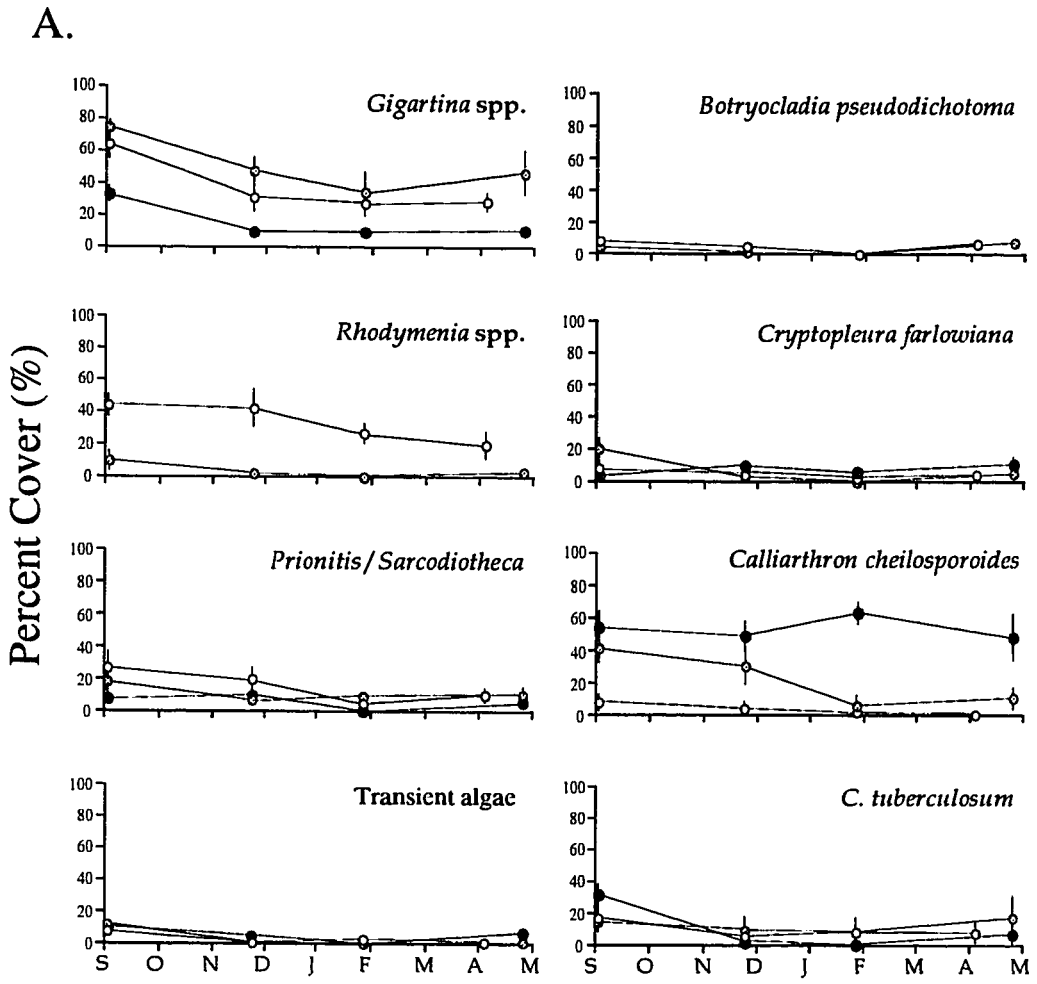
* only observed epiphytically

Appendix 2 (cont.)

A. Category	Site		
	MBA	LP	OP
Phaeophyta (cont.)			
Desmarestia ligulata var. *ligulata*	rare	rare	rare
Dictyoneurum californicum	-	uncommon	uncommon
Dictyoneuropsis reticulatum	uncommon	rare	-
Egregia menziesii	rare	rare	uncommon
Laminaria setchellii	-	rare	rare
Macrocystis pyrifera	rare	rare	rare
Spermatophyta			
Phyllospadix scouleri	rare	uncommon	rare

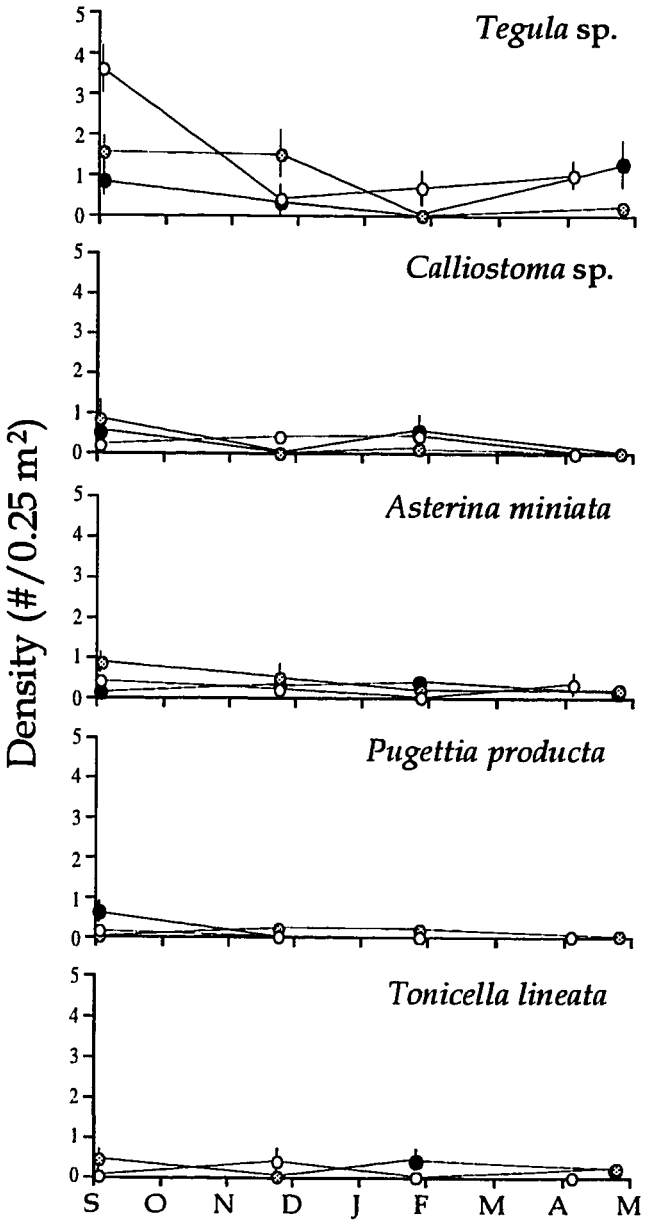
B. Category	Site		
	MBA	LP	OP
Asterina miniata	common	common	common
Astraea gibberosum	-	-	rare
Calliostoma sp.	common	common	common
Cryptochiton stelleri	rare	-	-
Pisaster giganteous	rare	-	-
Pugettia producta	uncommon	common	uncommon
Tegula sp.	common	common	common
Tonicella lineata	uncommon	common	common

Appendix 3. Abundance of (A) algae and (B) herbivores at MBA (○), LP (⊛), and OP (●) between September 1994 and May 1995 ($\bar{x} \pm SE$, n = 7). Algae are expressed as percent covers; herbivores as densities.



Appendix 3 (cont.).

B.



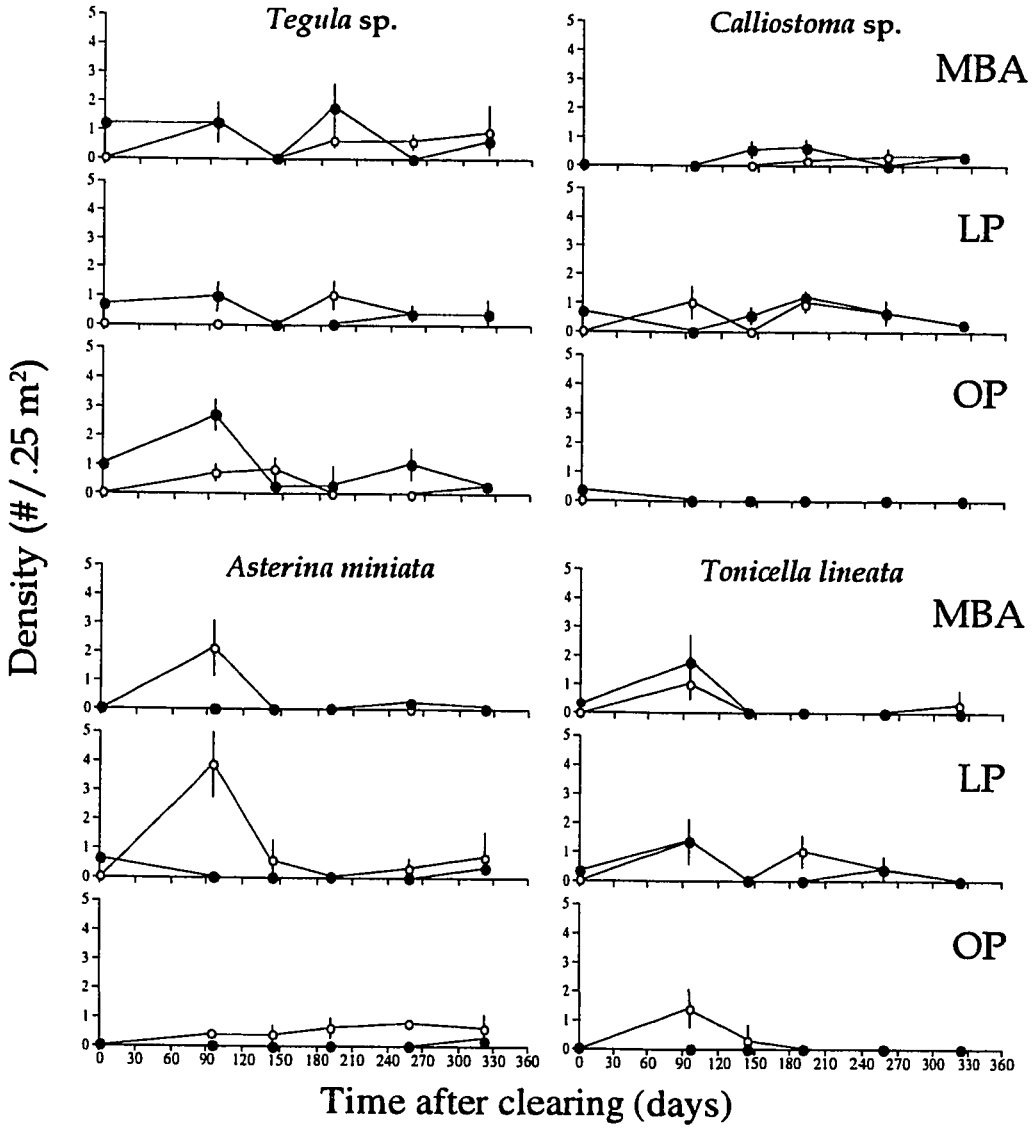
Appendix 4. Analysis of variance for the effect of Site and Date on (A) percent cover of algal species, and (B) density of herbivore species, at MBA, LP, and OP, between September 1994 and May 1995. Contrasts used Dunn-Sidak corrected alpha values. Asterisks indicate taxa that were not present at all three sites, resulting in decreased degrees of freedom (df).

	Source of variation			
A. Category	Site	Date	Site*Date	Contrasts
Botryocladia pseudodichotoma *	F = 0.69; df = 1; P > 0.4	F = 2.65; df = 3; P > 0.05	F = 0.32; df = 3; P > 0.8	
Calliarthron cheilosporoides	F = 52.65; df = 2; P < 0.0001	F = 2.18; df = 3; P > 0.9	F = 1.87; df = 6; P > 0.9	MBA < LP < OP
C. tuberculosum	F = 1.43; df = 2; P > 0.2	F = 5.43; df = 3; P < 0.002	F = 1.21; df = 6; P > 0.3	S > N = J = A
Cryptopleura farlowiana	F = 2.59; df = 2; P > 0.05	F = 3.78; df = 3; P < 0.025	F = 3.13; df = 6; P < 0.01	MBA: S = N = J = A LP: S > N = J = A OP: S = N = J = A S: MBA < LP > OP N: MBA = LP = OP J: MBA = LP = OP A: MBA = LP < OP
Gigartina spp.	F = 17.55; df = 2; P < 0.0001	F = 10.03; df = 3; P < 0.0001	F = 0.32; df = 6; P > 0.9	MBA = LP > OP S > N = J = A
Prionitis spp.	F = 9.91; df = 2; P < 0.001	F = 3.74; df = 3; P < 0.025	F = 1.43; df = 6; P > 0.2	MBA > LP > OP S = N = J = A S > J
Rhodymenia spp. *	F = 65.82; df = 1; P < 0.0001	F = 3.23; df = 3; P < 0.05	F = 0.94; df = 3; P > 0.4	MBA > LP S = N = J = A S > J

	Source of variation			
B. Category	Site	Date	Site*Date	Contrasts
Asterina miniata	F = 1.86; df = 2; P > 0.15	F = 0.68; df = 3; P > 0.5	F = 1.29; df = 6; P > 0.25	
Calliostoma sp.	F = 0.22; df = 2; P > 0.8	F = 1.81; df = 3; P > 0.15	F = 1.73; df = 6; P > 0.15	
Pugettia producta	N/A	N/A	N/A	
Tegula sp.	F = 3.09; df = 2; P > 0.05	F = 8.55; df = 3; P < 0.0001	F = 2.22; df = 6; P > 0.05	S > N = J = A
Tonicella lineata	N/A	N/A	N/A	

Appendix 5. (A) Density of herbivores and (B) recovery of turf algae, ($\bar{x} \pm$ SE. n = 3) in clearings (○) and control plots (●) as a function of time after clearing, at MBA, LP, and OP.

A.



Gigartina spp. recovered by day 92 at OP, and by day 192 at MBA and LP. Recovery of foliose algae other than *Gigartina* spp. (assorted foliose algae) was rapid at MBA and LP, but was not apparent at OP by the end of the study. The lack of recovery of assorted foliose algae at OP was due to the dynamics of *Cryptopleura farlowiana*. *Cryptopleura farlowiana* comprised almost all of the cover of assorted foliose algae in control plots at OP, but was not observed in the clearings at OP until day 345 (notice final sampling period at MBA was on day 325, but was on day 345 at LP and OP). *Cryptopleura farlowiana* was almost entirely absent from control plots at MBA and LP, and was not observed in the clearings at these sites during the study.

Recovery of *Prionitis* spp. and *Sarcodiotheca gaudichaudi* differed from other foliose algae and were analyzed separately. The percent cover of both taxa increased rapidly in the clearings, surpassing the percent cover of these taxa in the control plots by day 92. High recruitment of *Prionitis* spp. and *Sarcodiotheca gaudichaudi* accounted for much of the rapid recovery of bare substrate at MBA by day 141. Both taxa maintained highest cover in clearings for most of the study, but were present in the control plots at each site.

Transient algae (as described earlier) recruited heavily to the clearings at each site, but rarely to control plots. The cover of *Gymnogongrus leptophyllus* was the highest of all transient species and was observed in the clearings at each site. *Gymnogongrus leptophyllus* was also observed in control plots at LP on day 345, following disturbance to these plots on day 256 (notice high percent cover of bare substrate at LP on day 256). *Holmesia californica*, *Rhodoglossum roseum*, and *Pseudogloiophloea confusa* were often observed in cleared plots at MBA, LP, and OP, but were never observed in control plots.

Appendix 5 (cont.).

B.